BORROR AND DELONG'S INTRODUCTION TO THE

STUDY OF INSECTS

7th Edition

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Abbreviations Used in the Figures

The following list includes all the abbreviations used in the figures in Chapters 3 through 35. The abbreviations used on wing drawings for the veins and cells (using the Comstock-Needham terminology) are not listed in the figure legends, but are included in the following list. Subscript numerals are used to designate branches of the longitudinal veins. Such numerals are often used to designate the particular thoracic segment on which a structure is located (1, designating the prothorax; 2, the mesothorax; and 3, the metathorax). Subscript numerals are occasionally used to designate the particular abdominal segment on which a sclerite is located.

a, anal vein
A, anal vein, anal cell
ab, abdomen, opisthosoma
ac, accessory, lanceolate, or subanal vein
Ac, anal crossing (A branching posteriorly from Cu, often called the cubito-anal cross vein)
acc, accessory cell
acg, accessory gland
acg, accessory gland
acl, antennal club
aclp, anteclypeus
acr, acrostichal bristles
acs, acrosternite
act, acrotergite
acv, anterior cross vein
adf, adfrontal area
aed, aedeagus
af, antennal fossa
agr, scrobe, groove in beak for reception of antenna
al, anal lobe
alp, anal loop
alu, alula
am, axillary muscle
an, antenodal cross vein
AN, alinotum
anc, anal cleft
ancs, antecostal suture
anp, anal plate
anr, anal ring
ans, anus
ant, antenna
antc, antecosta
antl, antennule
ao, dorsal aorta
aos, anterior oblique sulcus on mesepisternum
ap, appendix
AP, apical cell
apc, apical cross vein
apd, apodeme
apo, apophysis
ar, arista
arc, arculus
are, areolet
aro, arolium
art, point of articulation
as, antennal sulcus, anterior spiracle
asc, antennal sclerite
ask, antennal socket
asp, apical spur
aspr, anterior spiracle
at, alimentary tract
ata, anterior tentorial arm
atb, anal tube
atp, anterior tentorial pit
au, auricle
av, auxiliary vein
aw, anterior wart
awp, anterior notal wing process
ax, axilla
AX, axillary cell
axc, axillary cell
axcr, axillary cord
axs, axillary sclerite
axv, axillary vein

B, basal cell
ba, basalare
BA, basal anal cell, basal areole
bc, bursa copulatrix
bcv, bridge cross vein
bg, book gills
bk, beak, proboscis, rostrum, or snout
bl, blastoderm
bln, banksian line
bm, basal medial cell, basement membrane
bm-cu, basal mediocubital cross vein
bms, basalar muscle
bp, brood pouch
br, brain or basal radial cell
brv, bridge vein
bt, breathing tube
buc, buccula or bucca
bv, basal vein
bvn, brace vein

c, costal vein
C, costal vein, costal cell
ca, corpus allatum
cal, calypter or squama
cb, corbicula
cbr, costal break
cc, crystalline cone
cd, cardo
cec, circumesophageal connective
cen, cenchri
cg, cerebral ganglion
ch, chelicera
cho, chorion
chp, cheliped
cl, clypeus, clavus
cla, clasper
clc, movable spines or calcaria
clm, calamistrum
clp, clypeus
clpl, clypellus
cls, claval suture
clt, claw tuft, clypeal tubercle
clv, claval vein
cm, gastric caeca or caecum
cn, colon
cna, cornea
cnge, corneagenous cells
cnu, cleavage nuclei
colm, collum, tergite of the first body segment
com, commissural trachea
comn, tritocerebral commissure
cor, corim
covd, common oviduct
cp, crop
cph, prosoma or cephalothorax
cpl, cortical cytoplasm
cr, cercus, lateral caudal filament, superior appendage
crb, cribellum
cre, cremaster
crl, crystalline lens
crn, cornicle
cro, crochets
crp, carapace
cs, coronal suture
csp, cusp of mandible, caudal spiracle
cu, cubital vein
Cu, cubital vein

cua$_1$, anterior cubital cell
cuf, cubital fork (fork of CuA)
cun, cuneus
cup, posterior cubital cell
CuP, posterior cubital vein
cut, cuticle
cva, clava
cvs, cervical sclerite
cvx, cervix
cx, coxa
cxc, coxal cavity
cxg, groove in coxa
cxp, coxopodite of abdominal appendages

d, discoidal or intercostal vein
D, discal cell, or discoidal cell
dc, dorsocentral bristles
dcv, discal cross vein
dlm, dorsal longitudinal muscle
dm, domelike layer of cuticle over nerve ending, or discal medial cell
dm-cu, discal medio-cubital cross vein
do, dorsal ostiole
dp, distal process of sensory cell
DSJ, disjugal furrow
dta, dorsal tentorial arm
dtra, dorsal trachea

e, eye, compound eye
ec, eye cap
ect, ectoderm
ef, epigastric furrow
eg, egg
ejd, ejaculatory duct
el, elytron
emb, embolium
emp, empodium
en, endophallus
end, endocuticle, endoderm
endr, endodermal rudiments
enl, endite lobe
enp, endopodite
ep, epidermis
epcr, epicranium
epg, epigynum
eph, epipharynx
epi, epicuticle
epm, epimeron
epp, epipleurite
epr, epistomal ridge
eps, episternum
ept, epiproct, median caudal filament, or inferior appendage
es, epistomal sulcus
eso, esophagus
ex, exuvium
exl, exite lobe
exm, extensor muscle
exo, exocuticle
exp, exopodite

f, frenulum
fa, face
fb, frontal bristles
fc, food channel
fch, filter chamber
fcn, frontal ganglion connective
ff, facial fovea
fg, frontal ganglion
fib, fibula
fl, flagellum
flb, flabellum
flm, flexor muscle
fm, femur
fmb, femoral bristles
fn, fang of chelicera
fob, fronto-orbital bristles
fon, fontanelle
for, foramen magnum
fr, frons
frl, frontal lunule
fs, frontal suture
fu, sternal apophysis, furca
fun, funiculus or funicle
fv, frontal vitta

g, galea
gap, gonapophysis
gc, genal comb
gcl, germ cell
gcx, gonocoxa
ge, gena
gen, male copulatory apparatus
gf, genital forceps
gh, gland hair
gi, gills
gl, glossa
glc, gland cell
gld, duct of gland cell
gls, gland spines
glt, gland tubercle
gn, ganglion of ventral nerve cord
gna, gnathochilarium
gon, gonangulum
gpl, gonoplacs
gr, gill remnants
gs, gular suture
gst, gonostylus
gt, genal tooth
gu, gula
gvp, genovertical or orbital plate

h, humeral cross vein
hal, haltere
hb, humeral bristles
hbr, hypostomal bridge
hc, humeral callus
hcl, hypostigmatic or truss cell
hd, head
hg, anterior portion of the hindgut
ho, horn
hp, humeral plate
hr, heart
hst, haustellum
hv, humeral or recurrent vein
hyb, hypopleural bristles
hyp, hypopharynx, intermediate stylet
hypl, hypopleuron

iab, intra-alar bristles
iap, interior appendage (paraproct)
iar, interantennal ridge
ias, interantennal suture
iep, infraepisternum
il, ileum
ism, intersegmental membrane
it, intercalated triangle
ivb, inner vertical bristles

j, jugum
jl, jugal lobe

l, leg
L, length, lanceolate
lba, labial articulation
lbl, labellum
lbm, labium, ventral stylet
lbn, labial nerve
lbr, labrum, rostrum
lbrn, labral nerve
lc, lacinia
lct, layer of the cuticle
lg, ligula, median lobe
ll, lamina lingualis
lo, lorum
lp, labial palp
LP, lateral plate
ls, labial suture
lst, lateral setae
ltra, main longitudinal tracheal trunk

m, medial cross vein, mouth, or recurrent nerve
M, medial vein, medial cell
ma, mandibular articulation
MA, anterior media
MC, marginal cell
mcf, median caudal filament
mcp, micropyle
md, mandible
MD, median cell
mdn, mandibular nerve
mdp, median plate (of wing), middle plate (of embryo)
mdu, microduct
mdv, median vein
mem, membrane
met, metasomatic segment
mf, medial fork (fork of MP$_2$)
mg, midgut or mesenteron
mh, movable hook or palp
ml, median lobe
mm, marginal macroduct
mn, mentum
mo, mouth
mp, mouthparts
MP, posterior media
mpb, mesopleural bristles
mpo, marginal 8-shaped pore
ms, mesoderm
msd, mesoderm
msl, mesosternal lobe
mspl, medial supplement
mst, mental seta
mt, Malpighian tubule
mts, metatarsus or first tarsal segment
mu, mucro
mv, marginal or radial vein
mx, maxilla, dorsal stylet
mxa, maxillary articulation
mxl, maxillary lobe
mxn, maxillary nerve
mxp, maxillary palp
mxt, maxillary tentacle

n, notum
nb, notopleural bristles
nc, ventral nerve cord
nod, nodus
n$_1$l, pronotal lobe
npl, notopleuron
npls, notopleural suture
nt, notaulus
nu, nucleus
nv, neuron

o, opening
ob, ocellar bristles
obv, oblique vein
oc, ocellus
ocp, occiput
ocpd, ocellar pedicel
ocs, ocular sulcus
ocg, occipital ganglion
og, optic ganglion
op, operculum
opl, optic lobe
opt, ocular point
orp, orbital plate
os, occipital sulcus
osm, osmeterium (scent gland)
ot, ocellar triangle

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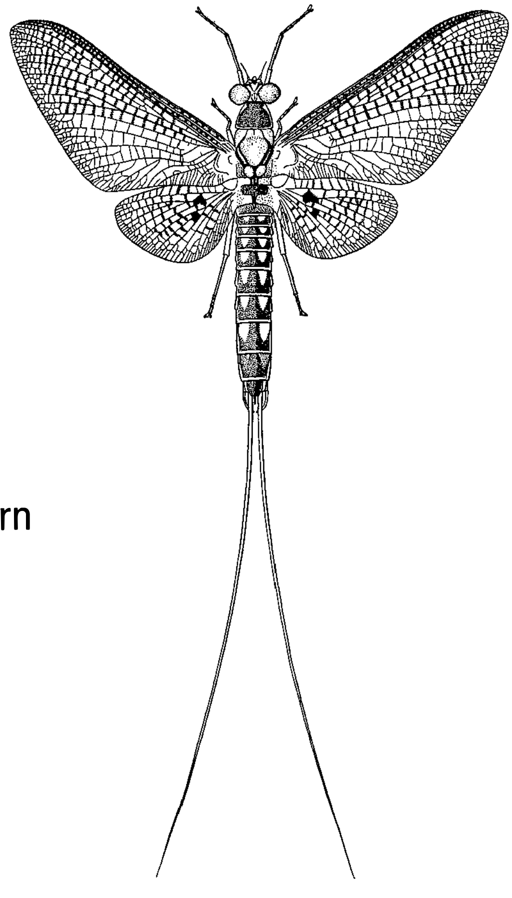

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Preface

An Introduction to the Study of Insects: this is the seventh edition of a textbook that has been widely used in entomology classes in North America over more than 50 years. Its value has been demonstrated by the fact that it retains a prominent place on the bookshelves of professional entomologists, long after their first exposure to insects in class. Because the book has been widely known by the names of its first two authors, we are adding their names to the title. The contributions of these two men, in both style and substance, will still be immediately apparent to knowledgeable readers even though the formal authorship has now passed on to subsequent generations. We have prepared this new edition in recognition of the important role the text has played in the education of biologists of all specializations and in the hope that it can continue to play that role in the future. NFJ clearly recalls the nights and weekends spent at Cranberry Lake Biological Station in the Adirondack Mountains of New York, poring over this book in the excitement of new discoveries and with an ever-growing appreciation for the diversity of insects. CAT, too, was greatly influenced by Borror and DeLong, but in a more direct way. He took undergraduate courses from both of them and quickly abandoned his original goals in herpetology when exposed to "the wonderful world of insects" in a beginning entomology course taught by Borror.

In this new edition we have concentrated our attention on the subject of insect systematics. The most obvious changes in content are the addition of a chapter for a newly described order, the Mantophasmatodea, and the subordination of the Homoptera into an enlarged concept of the order Hemiptera. Beyond that, though, the classification of nearly every order has been modified, sometimes substantially, to reflect new discoveries and scientific hypotheses. The chapter on beetles has been updated considerably to reflect the changes in our understanding of the diversity and phylogeny of Coleoptera. Many new families have been added throughout the book, some reflecting revised classifications, but many the result of the discovery of new groups within the United States and Canada, particularly from the New World tropics. These include the families Platystictidae (Odonata), Mackenziellidae (Collembola), Mantoididae

(Mantodea), and Fauriellidae (Thysanoptera), to name just a few. Changes in classifications also have been brought about by the widespread adoption of the methods of phylogenetic systematics and their application to a new source of information on insect relationships, molecular sequence data. Although these new data will not help the beginning student to identify specimens, the results of molecular analyses are beginning to substantively contribute to the the development of a robust and predictive classification. Thus, our best hypotheses of the phylogeny of insects has changed rather drastically from the last edition, incorporating molecular data. The most conspicuous change is the recognition that the order Strepsiptera is most closely related to the true flies (Diptera), rather than to the Coleoptera.

As we turn to focus our efforts on the issues of insect systematics and evolution, a better appreciation for the magnitude of the diversity of life and Earth as well as the immediate and long-term threats to that same diversity have become important societal issues. It is our hope that this text will continue to have an important role to play in understanding and preserving this diversity for the benefit of all.

Donald Joyce Borror was the senior author on the first six editions of this book. He died before the last edition was printed. He was unsurpassed in his ability to construct keys for the identification of insects and was constantly modifying them to make certain that the user would arrive at the correct taxon. His discussion of the various families, containing facts gleaned from the literature, is amazing, considering that it was done before computers were available. Furthermore, the entire manuscripts were typed by Borror on an old manual typewriter. He was well-versed in Greek and Latin and also knew shorthand. His influence was missed in preparation of this edition, and we hope that it would have met with his approval.

C. A. T.
N. F. J.

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We also gratefully acknowledge the services of Kathy Royer, Sue Ward, and Bruce Leach for help with preparation of the manuscript and in locating references. We accept the responsibility for all errors and cases in which the keys fail to work, or taxa are omitted or misplaced. We hope that these are few and not serious.

Table of Contents

1

Insects and Their Ways

The science of taxonomy takes as its arbitrary starting point the publication of the 10th edition of Linnaeus's *Systema Naturae* in 1758. More than two centuries later, nearly one million species of insects have been described and named. Biology in the 21st century has changed in many fundamental ways, led primarily by the revolution in molecular biology. Yet the study of diversity of life on Earth has not faded into the past. Rather, it has become reinvigorated by advances in other sciences and in technology. We continue to discover new species at an increasing rate, even as habitat destruction by the growing human population brings the threat of extinction. In 2002, entomologists announced the discovery of a new order of insects, the Mantophasmatodea, illustrating that our understanding of even the major groups is imperfect. Our goal in writing this book is to provide an introduction to the diversity of insects and their relatives and a resource for identifying the fauna of temperate North America. We thus hope to encourage the study of these fascinating creatures so that we all may better understand the world in which we live.

Insects are the dominant group of animals on Earth today. They far outnumber all other terrestrial animals, and they occur practically everywhere. Several hundred thousand different kinds have been described—three times as many as there are in the rest of the animal kingdom—and some authorities believe the total number of different kinds may approach 30 million. More than a thousand kinds may occur in a fair-sized backyard, and their populations often number many millions per acre.

A great many insects are extremely valuable to humans, and society could not exist in its present form without them. By their pollinating activities, they make possible the production of many agricultural crops, including many orchard fruits, nuts, clovers, vegetables, and cotton; they provide us with honey, beeswax, silk, and other products of commercial value; they serve as food for many birds, fish, and other beneficial animals; they perform valuable services as scavengers; they help keep harmful animals and plants in check; they have been useful in medicine and in scientific research; and people in all walks of life look on them as interesting animals. A few insects are harmful and cause enormous losses each year in agricultural crops and stored products, and some insects transmit diseases that seriously affect the health of humans and other animals.

Insects have lived on Earth for about 350 million years, compared with less than 2 million for humans. During this time, they have evolved in many directions to become adapted to life in almost every type of habitat (with the notable and puzzling exception of the sea) and have developed many unusual, picturesque, and even amazing features.

Compared with humans, insects are peculiarly constructed animals. Humans might think of them as inside out, because their skeleton is on the outside, or upside down, because their nerve cord extends along the lower side of the body and the heart lies above the alimentary canal. They have no lungs, but breathe through a number of tiny holes in the body wall—all behind the head—and the air entering these holes is distributed over the body and directly to the tissues through a multitude of tiny branching tubes. The heart and blood are unimportant in transporting oxygen to the tissues. Insects smell with their antennae, some taste with their feet, and some hear with special organs in the abdomen, front legs, or antennae.

In an animal whose skeleton is on the outside of the body, the mechanics of support and growth limit the animal to a relatively small size. Most insects *are* relatively small: Probably three fourths or more are less than 6 mm in length. Their small size enables them to live in places that would not be available to larger animals.

Insects range in size from about 0.25 to 330 mm in length and from about 0.5 to 300 mm in wingspread; one fossil dragonfly had a wingspread of over 760 mm! Some of the longest insects are very slender (the 330-mm insect is a walking stick occurring in Borneo), but some beetles have a body nearly as large as one's fist. The largest insects in North America are some of the moths, with wingspreads of about 150 mm, and the walking stick, with a body length of about 150 mm.

The insects are the only invertebrates with wings, and these wings have had an evolutionary origin different from that of the vertebrates. The wings of flying vertebrates (birds, bats, and others) are modifications of the forelimbs; those of insects are structures *in addition to* the paired "limbs," and might be likened to the wings of the mythical horse Pegasus. With wings, insects can leave a habitat when it becomes unsuitable; adult aquatic insects, for example, have wings when adult, and if their habitat dries up they can fly to another habitat. Under similar adverse conditions, fish and other aquatic forms usually perish.

Insects range in color from very drab to brilliant; no other animals on Earth are more brilliantly colored than some of the insects. Some insects, such as the Japanese beetle and the morpho butterfly are glittering and iridescent, like living jewels. Their colors and shapes have inspired artists for millennia.

Some insects have structures that are amazing when we compare them to vertebrates. The bees and wasps and some of the ants have their ovipositor, or egg-laying organ, developed into a poison dagger (sting) that serves as an excellent means of offense and defense. Some ichneumonids have a hairlike ovipositor 100 mm long that can penetrate solid wood. Some snout beetles have the front of the head drawn out into a slender structure longer than the rest of the body, with tiny jaws at the end. Some flies have their eyes situated at the ends of long, slender stalks, which in one South American species are as long as the wings. Some of the stag beetles have jaws half as long as their bodies and branched like the antlers of a stag. Certain individuals in some of the honey ants become so engorged with food that their abdomens become greatly distended. These serve as living storehouses of food, which they regurgitate "on demand" to other ants in the colony.

Insects are cold-blooded creatures. When the environmental temperature drops, their body temperature also drops, and their physiological processes slow down. Many insects can withstand short periods of freezing temperatures, and some can withstand long periods of freezing or subfreezing temperatures. Some insects survive these low temperatures by storing in their tissues ethylene glycol, the same chemical that we pour into our car radiators to protect them from freezing during the winter.

Insect sense organs often seem peculiar compared with those of humans and other vertebrates. Many insects have two kinds of eye—two or three simple eyes located on the upper part of the face and a pair of compound eyes on the sides of the head. The compound eyes are often very large, occupying most of the head, and may consist of thousands of individual "eyes." Some insects hear by means of eardrums, whereas others hear by means of very sensitive hairs on the antennae or elsewhere on the body. An insect that has eardrums may have them on the sides of the body at the base of the abdomen (grasshoppers) or on the front legs below the "knee" (katydids and crickets).

The reproductive powers of insects are often tremendous; most people do not realize just how great they are. The capacity of any animal to build up its numbers through reproduction depends on three characteristics: the number of fertile eggs laid by each female (which in insects may vary from one to many thousands), the length of a generation (which may vary from a few days to several years), and the proportion of each generation that is female and will produce the next generation (in some insects there are no males).

An example that might be cited to illustrate insects' reproductive powers is *Drosophila*, the fruit fly that has been studied by so many geneticists. These flies develop rapidly and under ideal conditions may produce 25 generations in a year. Each female will lay up to 100 eggs, of which about half will develop into males and half into females. Suppose we start with a pair of these flies and allow them to increase under ideal conditions, with no checks on increase, for a single year—with the original and each female laying 100 eggs before she dies and each egg hatching, growing to maturity, and reproducing again, at a 50:50 sex ratio. With 2 flies in the first generation, there would be 100 in the second, 5000 in the third, and so on, with the 25th generation consisting of about 1.192×10^{41} flies. If this many flies were packed tightly together, 1000 to a cubic inch, they would form a ball of flies *96,372,988 miles in diameter*—or a ball extending approximately from Earth to the sun!

Throughout the animal kingdom, an egg usually develops into a single individual. In humans and some other animals one egg occasionally develops into two individuals (that is, identical twins) or, on rare occasions, three or four. Some insects carry this phenomenon of polyembryony (more than one young from a single egg) much further; some platygastrid wasps have as many as 18, some dryinid wasps have as many as 60, and some encyrtid wasps have more than 1000 young developing from a single egg. A few insects have another unusual method of reproduction, paedogenesis (reproduction by larvae). This occurs in the gall gnat genus *Miastor* and the beetle genera *Micromalthus*, *Phengodes*, and *Thylodrias*.

In the nature of their development and life cycle, insects run the gamut from very simple to complex and even amazing. Many insects undergo very little change as they develop, with the young and adults having similar habits and differing principally in size. Most insects, in contrast, undergo in their development rather remarkable changes, both in appearance and in habits. Most people are familiar with the metamorphosis of insects and possibly think of it as commonplace, which, as a matter of fact, it is. Consider the development of a butterfly: An egg hatches into a wormlike caterpillar; this caterpillar eats ravenously and every week or two sheds its exoskeleton; after a time it becomes a pupa, hanging from a leaf or branch; and finally a beautiful, winged butterfly emerges. Most insects have a life cycle like that of a butterfly; the eggs hatch into wormlike larvae, which grow by periodically shedding their outer exoskeleton (together with the linings of the foregut, hindgut, and breathing tubes), finally transforming into an inactive pupal stage from which the winged adult emerges. A fly grows from a maggot; a beetle grows from a grub; and a bee, wasp, or ant grows from a maggotlike larval stage. When these insects become adult, they stop growing; a little fly (in the winged stage) does not grow into a bigger one.

An insect with this sort of development (complete metamorphosis) may live as a larva in a very different type of place from that in which it lives as an adult. One common household fly spends its larval life in garbage or some other filth; another very similar fly may spend its larval life eating the insides out of a grub or caterpillar. The june beetle that flies against the screens at night spends its larval life in the ground, and the long-horned beetle seen on flowers spends its larval life in the wood of a tree or log.

Many insects have unusual features of structure, physiology, or life cycle, but probably the most interesting things about insects are what they do. In many instances the behavior of an insect seems to surpass in intelligence the behavior of humans. Some insects give the appearance of an amazing foresight, especially as regards laying eggs with a view to the future needs of the young. Insects have very varied food habits; they have some interesting means of defense; many have what might be considered fantastic strength (compared with that of vertebrates); and many have "invented" things we may think of as strictly human accomplishments. Some groups of insects have developed complex and fascinating social behavior.

Insects feed on an almost endless variety of foods, and they feed in many different ways. Thousands of species feed on plants, and practically every kind of plant (on land or in fresh water) is fed on by some kind of insect. The plant feeders may feed on almost any part of the plant; caterpillars, leaf beetles, and leafhoppers feed on the leaves, aphids feed on the stems, white grubs feed on the roots, certain weevil and moth larvae feed on the fruits, and so on. These insects may feed on the outside of the plant, or they may burrow into it. Thousands of insects are carnivorous, feeding on other animals; some are predators, and some are parasites. Many insects that feed on vertebrates are blood sucking; some of these, such as mosquitoes, lice, fleas, and certain bugs, not only are annoying pests because of their bites, but may serve as disease vectors. Some insects feed on dead wood; others feed on stored foods of all types; some feed on various fabrics; and many feed on decaying materials.

The digger wasps have an interesting method of preserving food collected and stored for their young. These wasps dig burrows in the ground, provision them with a certain type of prey (usually other insects or spiders), and then lay their eggs (usually on the body of the prey animal). If the prey animals were killed before being put into the burrows, they would dry up and be of little value as food by the time the wasp eggs hatched. These prey animals are not killed; they are stung and paralyzed, and thus "preserved" in good condition for the young wasps when they hatch.

Insects often have interesting and effective means of defense against intruders and enemies. Many "play dead," either by dropping to the ground and remaining motionless or by "freezing" in a characteristic position. Others are masters of the art of camouflage, being so colored that they blend with the background and are very inconspicuous; some closely resemble objects in their environment—dead leaves, twigs, thorns, or even bird droppings. Some insects become concealed by covering themselves with debris. Others that do not have any special means of defense very closely resemble another that does, and presumably are afforded some protection because of this resemblance. Many moths have the hind wings (which at rest are generally concealed beneath the front wings) brightly or strikingly colored—sometimes with spots resembling the eyes of a larger animal (for example, giant silkworm moths; see Figure 30–76)—and when disturbed display these hind wings; the effect may sometimes be enough to scare off a potential intruder. Some of the sound-producing insects (for example, cicadas, some beetles, and others) produce a characteristic sound when attacked, and this sound often scares off the attacker.

Many insects use a "chemical warfare" type of defense. Some secrete foul-smelling substances when disturbed; stink bugs, broad-headed bugs, lacewings, and some beetles might well be called the skunks of the insect world, because they have a very unpleasant odor. A few of the insects using such defensive mechanisms can eject the substance as a spray, in some cases even aiming it at an intruder. Some insects, such as the milkweed butterflies, ladybird beetles, and net-winged beetles, apparently have distasteful or mildly toxic body fluids, and predators avoid them.

Many insects inflict a painful bite when handled. The bite may be simply a severe pinch by powerful jaws, but the bites of mosquitoes, fleas, black-flies, assassin bugs, and many others are much like hypodermic injections; the irritation is caused by the saliva injected at the time of the bite.

Other means of defense include the stinging hairs some caterpillars have (for example, the saddleback caterpillar and the larva of the io moth), body fluids that are irritating (for example, blister beetles), death feigning (many beetles and some insects in other orders), and warning displays, such as eyespots on the wings (many moths and mantids) or other bizarre or grotesque structures or patterns.

One of the most effective means of defense insects possess is a sting, which is developed in the wasps, bees, and some ants. The sting is a modified egg-laying organ; hence only females sting. It is located at the posterior end of the body, so the "business" end of a stinging insect is the rear.

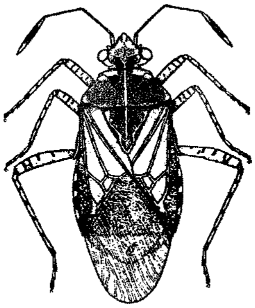
Insects often perform feats of strength that seem nearly impossible compared with those of human beings. It is not unusual for an insect to be able to lift 50 or more times its own weight, and researchers have found that some beetles, when rigged with a special harness, can lift more than 800 times their own weight. If they were as strong as such beetles, a human could lift some 60 tons, and an elephant could lift a fair-sized building! When it comes to jumping, many insects put our best Olympic athletes to shame. Many grasshoppers can easily jump a distance of 1 meter, which is comparable to a human long-jumping the length of a football field, and a flea jumping several inches up in the air is comparable to a human jumping over a 30-story building.

Many insects do things that we might consider strictly an activity of civilized humans or a product of our modern technology. Caddisfly larvae were probably the first organisms to use nets to capture aquatic organisms. Dragonfly nymphs, in their intake and expulsion of water to aerate the gills in the rectum, were among the first to use jet propulsion. Honey bees were air-conditioning their hives long before humans even appeared on Earth. Hornets were the first animals to make paper from wood pulp. Long before people began making crude shelters, many insects were constructing shelters of clay, stone, or "logs" (Figure 29–8), and some even induce plants to make shelters (galls) for them. Long before the appearance of humans on Earth, the insects had "invented" cold light and chemical warfare and had solved many complex problems of aerodynamics and celestial navigation. Many insects have elaborate communication systems, involving chemicals (sex, alarm, trail-following, and other pheromones), sound (cicadas, many Orthoptera, and others), behavior (for example, honey bee dance "language"), light (fireflies), and possibly other mechanisms.

These are only a few of the ways in which insects have become adapted to life in the world about us. Some of the detailed stories about these animals are fantastic and almost incredible. In the following chapters, we point out many of the interesting and often unique features of insect biology—methods of reproduction, ways of obtaining food, techniques for depositing eggs, methods of rearing the young, and features of life history—as well as the more technical phases that deal with morphology and taxonomy.

2

The Anatomy, Physiology, and Development of Insects



A knowledge of anatomy and physiology is essential to an understanding of insects. It is also necessary to have names for structures in order to be able to talk about them. The nomenclature of insect anatomy should be viewed as a language, a tool, that makes precise discussions about insects possible, and not as a barrier to understanding. In fact, many of the terms (for example, *femur, trochanter, mandible*) have analogous meanings in the context of vertebrate anatomy. The terms that have special meanings in individual orders are discussed in the appropriate chapters. In addition, all terms used are defined in the glossary at the back of this book. Our primary purpose in this chapter is to provide the student with the basic understanding of insect anatomy necessary to use the rest of the book.

Insects are more or less elongate and cylindrical in form and are bilaterally symmetric; that is, the right and left sides of the body are essentially alike. The body is divided into a series of segments, the metameres, and these are grouped into three distinct regions or **tagmata** (singular, *tagma*): the head, thorax, and abdomen (Figure 2–1). The primary functions of the head are sensory perception, neural integration, and food gathering. The thorax is a locomotory tagma and bears the legs and wings. The abdomen houses most of the visceral organs, including components of the digestive, excretory, and reproductive systems.

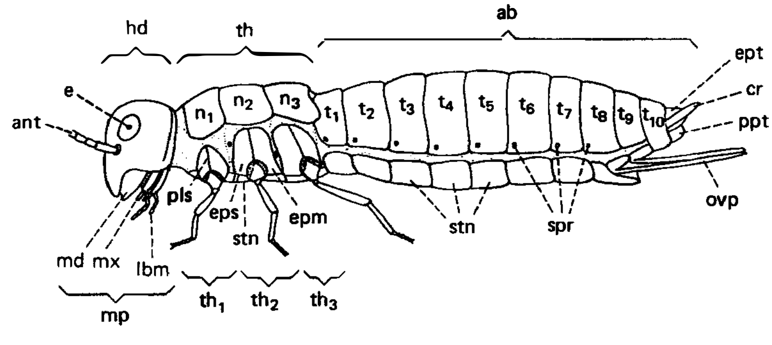


Figure 2–1 General structure of an insect. ***ab***, abdomen; *ant*, antenna; *cr*, cercus; *e*, compound eye; *epm*, epimeron; *eps*, episternum; *ept*, epiproct; *hd*, head; *lbm*, labium; *md*, mandible; *mp*, mouthparts; *mx*, maxilla; *n*, nota of thorax; *ovp*, ovipositor; *pls*, pleural suture; *ppt*, paraproct; *spr*, spiracles; $t_{1\text{-}10}$, terga; *th*, thorax; th_1, prothorax; th_2, mesothorax; th_3, metathorax. (Modified from Snodgrass, 1935, Principles of Insect Morphology, Cornell University Press.)

The Body Wall

The skeleton of an animal supports and protects the body, and transfers the forces generated by the contraction of muscles. One of the fundamental features of arthropods is the development of hardened plates, or **sclerites**, and their incorporation into the skeletal system of the animal. This is usually called an **exoskeleton**, because the sclerites are part of the outer body wall of the arthropod. In fact, however, arthropods also have an extensive endoskeleton of supports, braces, and ridges for the attachment of muscles. The characteristics of the body wall also influence the way in which substances such as water and oxygen move into and out of the animal.

The integument of an insect consists of three principal layers (Figure 2–2): a cellular layer, the epidermis; a thin acellular layer below the epidermis (that is, toward the inside of the animal), the basement membrane (or basal lamina); and another acellular layer, outside of and secreted by the cells of the epidermis, the cuticle.

The cuticle is a chemically complex layer, not only differing in structure from one species to another but even differing in its characteristics from one part of an insect to another. It is made up of chains of a polysaccharide, chitin, embedded in a protein matrix. Chitin primarily consists of monomers of the sugar N-acetylglucosamine (Figure 2–3). Individual chitin chains are intertwined to form microfibrils, and these microfibrils are often laid down in parallel in a layer called a *lamina*.

Chitin itself is a very resistant substance, but it does not make the cuticle hard. The hardness is derived from modifications of the protein matrix in which the microfibrils are embedded. The cuticle initially secreted by the epidermis, called *procuticle*, is soft, pliant, pale in color, and somewhat expandable. The formation of sclerites in this cuticle is the process of hardening and darkening, or sclerotization. This results from the formation of cross bonds between protein chains in the outer portions of the procuticle. Such sclerotized cuticle is called *exocuticle* (Figure 2–2, exo). Below the exocuticle may be unsclerotized cuticle called *endocuticle* (Figure 2–2, end). This pliant endocuticle forms the "membranes" that connect sclerites and can be resorbed into the body before molting.

Atop the endo- and exocuticle is a very thin, acellular layer, the epicuticle (Figure 2–2, epi). This itself consists of layers: those generally present are cuticulin,

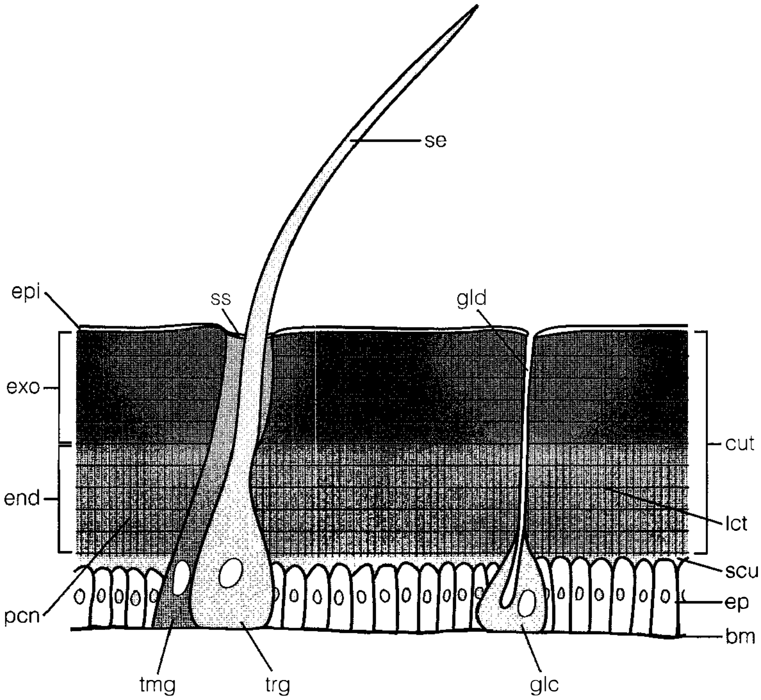


Figure 2–2 Structure of the body wall (diagrammatic). *bm*, basement membrane; *cut*, cuticle; *end*, endocuticle; *ep*, epidermis; *epi*, epicuticle; *exo*, exocuticle; *glc*, gland cell; *gld*, duct of gland cell; *lct*, layer of the cuticle; *pcn*, pore canal; *se*, seta; *ss*, setal socket; *tmg*, tormogen cell (which forms the setal socket); *trg*, trichogen cell (which forms the seta).

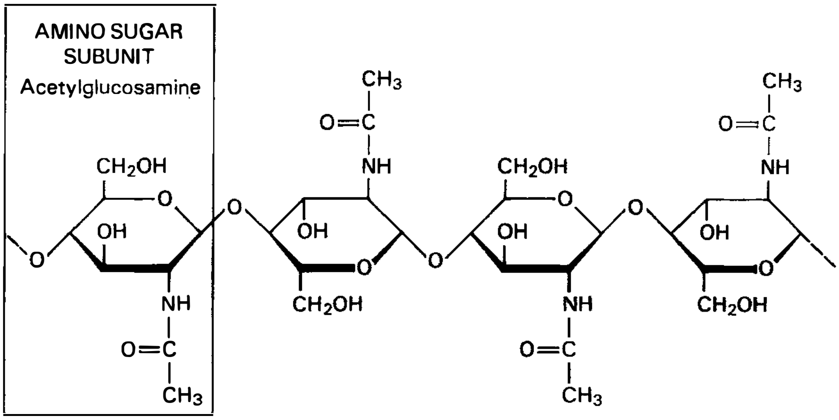


Figure 2–3 Chemical structure of chitin and its primary monomeric component, *N*-acetylglucosamine. (From Arms and Camp 1987.)

a wax layer, and a cement layer. The epicuticle contains no chitin. The wax layer is very important to terrestrial insects, because it serves as the primary mechanism to limit the loss of water across the body wall (both exocuticle and endocuticle are permeable to water). As a solid decreases in size (as measured by volume, surface area, or some linear dimension) the ratio of its surface-area to volume, that is, the relative amount of surface area, increases. Therefore, the loss of water across the body surface is relatively much more important to a small creature than to a large one. Many small terrestrial animals, such as snails and isopods, do not have such a protective wax layer, but these creatures usually live only in regions of high relative humidity, which decreases the rate at which water is lost from their body. The outermost cement layer is thought to protect the wax beneath from abrasion.

The sclerites of the body wall are often subdivided by grooves and crests, or may project into the body as internal struts. In general, an external groove marking an infolding of cuticle of the outer body wall is called a sulcus (plural, *sulci*) (Figure 2–4, su). The term suture, also very widely used, refers to a line of fusion between two formerly separated sclerites. The distinction is a subtle one and often difficult or impossible to make simply by looking at the external structure of a specimen. Therefore, in this book we generally use these terms more or less synonymously. The lines of inflection seen externally usually correspond to internal ridges, or costae (Figure 2–4, cos). The internal costae may serve as strengthening braces or as the sites of muscle attachment. An external crest may be referred to as a costa or carina (or any number of common English names such as *keel*). Internal projections of cuticle are also referred to as **apodemes** or **apophyses** (Figure 2–4, apo).

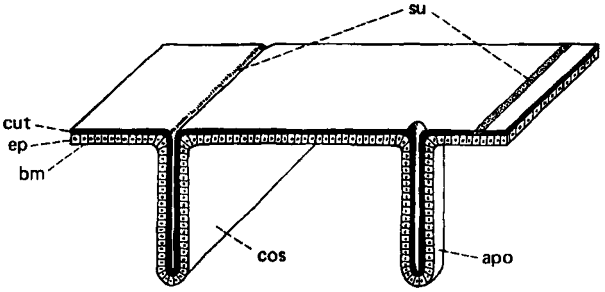


Figure 2–4 Diagram of external and internal features of the body wall. *apo*, apophysis; *bm*, basement membrane; *cos*, costa; *cut*, cuticle; *ep*, epidermis; *su*, sulcus or suture.

Abdomen

We begin our discussion of the three tagmata of insects with the abdomen because in contrast to the head and thorax, it is relatively simple in structure. Arthropods, like vertebrates, are built on a basic ground plan of repeated body segments, or metameres. These are most clearly visible in the abdomen. In general, the abdomen of an insect is made up of a maximum of 11 metameres (Figure 2–1, ab). Each metamere typically has a dorsal sclerite, the tergum (plural, *terga*; Figure 2–1, t_1–t_{10}; Figure 2–5A, t); a ventral sclerite, the sternum (plural, *sterna*; Figure 2–1, stn; Figure 2–5A, stn); and a membranous lateral region, the pleuron (plural, *pleura*; Figure 2–5A, plm). The openings to the respiratory system, the **spiracles** (Figure 2–1, spr), typically are

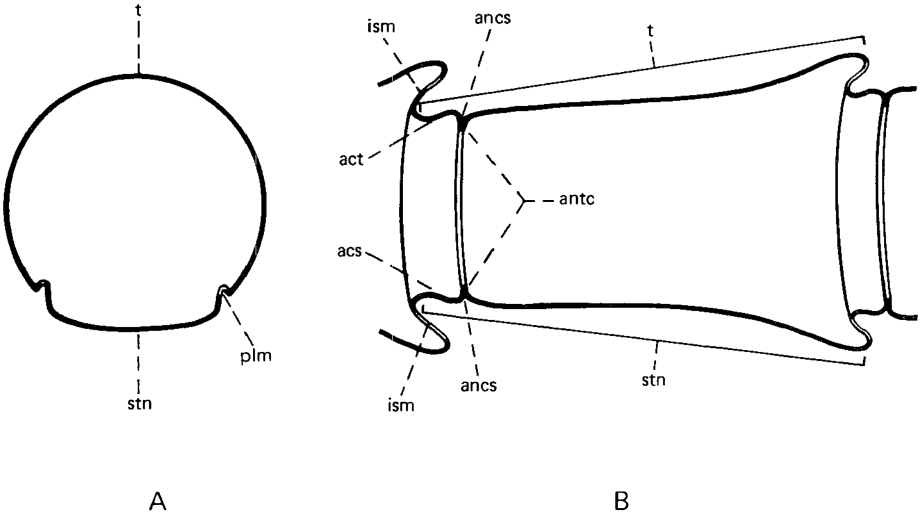


Figure 2–5 Structure of a typical abdominal segment (diagrammatic). A, Cross section; B, Sagittal section. *acs*, acrosternite; *act*, acrotergite; *ancs*, antecostal suture; *antc*, antecosta; *ism*, intersegmental membrane; *plm*, pleural membrane; *stn*, sternum; *t*, tergum.

located in the pleuron. Terga and sterna may be subdivided; these parts are referred to as **tergites** and **sternites**. Sclerites in the pleural wall are called **pleurites**.

This segmentation of the abdomen differs from that found in other nonarthropod protostomes such as the segmented worms (Annelida). In these, the externally visible grooves in the body wall delimiting the metameres serve as the points of attachment for the dorsal and ventral longitudinal muscles. In arthropods, these muscles attach to internal costae, the **antecostae**, which are located near, but not at, the anterior margins of the terga and sterna (Figure 2–5B, antc). Externally, the position of the antecosta is indicated by a groove, the **antecostal suture** (Figure 2–5B, ancs). The region of the tergum anterior to the antecostal sulcus is the **acrotergite** (Figure 2–5B, act). The corresponding region of the sternum is the **acrosternite** (Figure 2–5B, acs). The main dorsal longitudinal muscles extend between the antecostae of successive segments. Contraction of these muscles results in a telescoping, or retraction, of the abdominal segments. This body plan, in which the externally visible segmentation does not conform to the attachment of the longitudinal muscles, is known as **secondary segmentation**.

The genitalia of insects are generally located on or about abdominal segments 8 and 9. These segments have a number of specializations associated with copulation and oviposition; our discussion of them is therefore included in the section later on the reproductive systems. Segments 1–7, anterior to the genitalia, are the pregenital segments. In most adult winged insects, these segments have no appendages. In the primitively wingless insects,[1] the orders Microcoryphia and Thysanura, the ventral portion of a pregenital segment generally consists of a small medial sternum and two large plates laterad of the sternum, the **coxopodites** (see Figure 8-1B, cxp and stn). The coxopodites are remnants of the bases of the abdominal legs, and apically they bear a musculated **stylus** (Figure 8-1A,B, sty). The styli probably represent the apical portions of these legs (the telopods), but they are not segmented as are the thoracic legs. The styli generally function as sensory organs and also support the abdomen, much like the runners of a sled. Mesal to the styli are one or sometimes two pairs of eversible vesicles, which function in water absorption. They are everted from the body by hydrostatic pressure and retracted by muscles. In many cases the coxopodites and the sternum are fused into a single composite sclerite, the **coxosternum**.

Pregenital abdominal appendages are present in winged insects only in immature stages (with the exception of male Odonata). In embryos, the appendages of the first abdominal segment, known as **pleuropodia**, are present. These are glandular structures and are lost before the insect hatches from the egg. The larvae of some Neuroptera (Figure 27-6A–C) and Coleoptera (Figures 26–19A,B, 26–21A) bear lateral styluslike structures that have variously been interpreted as rep-

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[1] As we describe in Chapter 6, we are distinguishing between the terms *Hexapoda* and *Insecta*, restricting the latter to refer to the Pterygota, Thysanura, and Microcoryphia.

resenting leg rudiments, styli, or secondarily developed gills. The nymphs of Ephemeroptera bear a series of platelike gills along the upper lateral portions of the body (Figure 9-2). Again, from just what structures these gills were derived and what their serial homologs may be on the thorax have been considerably debated.

The immature stages of a number of orders have prolegs on the pregenital segments. These are typically fleshy, short appendages that are important in walking or crawling (see, for example, Figures 30-3, prl; 30–74, ventral, plg; and 28–37). Hinton (1955) concluded that prolegs had evolved independently a number of times; others, such as Kukalová-Peck (1983), interpret these structures as modified abdominal legs, both homologous between orders and serially homologous with the segmented thoracic legs.

The postgenital segments are typically reduced in insects. Among hexapods, the Protura are unique in that they have 12 well-developed segments in the abdomen (representing 11 metameres and an apical nonmetameric telson). In general, the only indications of an 11th segment among insects are a dorsal sclerite, the epiproct, and two lateral sclerites, the paraprocts (Figure 2–1, ept, ppt). Between them are inserted the appendages of the apical abdominal segment, the **cerci** (singular, *cercus*). Typically the cerci are sensory organs, but in some cases they are modified as organs of defense (as in the forceps of Dermaptera, Figures 15–1 and 15–2) or may be specialized as accessory copulatory organs. Very often the apical abdominal segments are highly reduced or normally retracted within the body.

Thorax

The **thorax** is the locomotory tagma of the body, and it bears the legs and wings. It is made up of three segments, the anterior **prothorax, mesothorax,** and posterior **metathorax** (Figure 2–1, th_1–th_3). Among insects, a maximum of two pairs of spiracles open on the thorax, one associated with the mesothorax, one with the metathorax. The mesothoracic spiracle serves not only that segment but also the prothorax and head. The terga of the thorax are typically called nota (singular, *notum*). Among present-day insects, wings are borne at most on the mesothoracic and metathoracic segments; these two segments are collectively called the **pterothorax** to reflect this (*pteron*, Greek for "wing"). These segments have several modifications associated with flight that are not shared with the prothorax.

The prothorax is connected to the head by a membranous necklike region, the cervix (Figure 2–6, cvx). Dorsal longitudinal muscles extend from the mesothorax through the prothorax and insert on the head; the pronotum has no antecosta. Movements of the head coordinate with the rest of the body by one or two pairs of **cervical sclerites** (Figure 2–6, cvs) that articulate with the prothorax posteriorly and the head anteriorly.

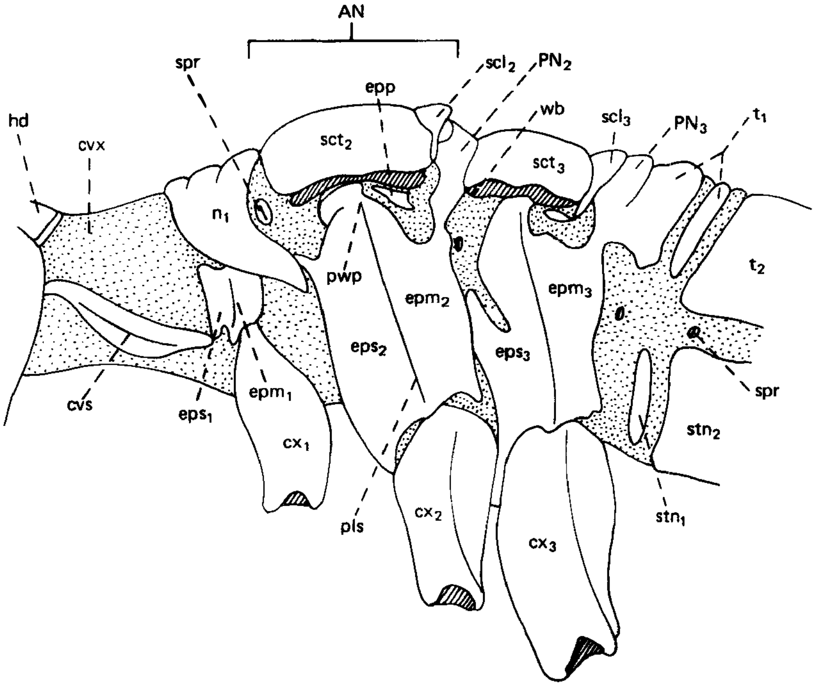

Figure 2–6 Thorax of *Panorpa*, lateral view. *AN*, alinotum; *cvs*, cervical sclerite; *cvx*, cervix; *cx*, coxa; *epm*, epimeron; *epp*, epipleurite; *eps*, episternum; *hd*, head; n_1, pronotum; *pls*, pleural suture; *PN*, postnotum; *pwp*, pleural wing process; *scl*, scutellum; *sct*, scutum; *spr*, spiracle; *stn*, abdominal sternum; *t*, abdominal tergum; *wb*, base of wing. (Redrawn from Ferris and Rees 1939.)

The system of secondary segmentation just described in reference to the abdomen is modified in the pterothorax to accommodate the flight musculature. The dorsal longitudinal muscles of the meso- and metathorax are greatly enlarged and are involved in depression (downward movement) of the wings (Figure 2–7B, dlm). As a corollary, the sites of insertion of these muscles—that is, the antecostae of the mesothorax, metathorax, and first abdominal segments—are also greatly enlarged and project downward within the thorax and base of the abdomen. These enlarged antecostae are called the *first, second,* and *third* phragmata respectively (singular, *phragma*; Figure 2–7B, ph$_1$–ph$_3$). Externally, the mesonotum and metanotum are typically divided transversely by a sulcus that gives added flexibility. The sulcus divides each notum into an anterior scutum (Figure 2–6, sct$_2$, sct$_3$) and a posterior scutellum (Figure 2–6, scl$_2$, scl$_3$). In addition, the portions of the notum bearing the second and third phragma are often separated from the following scutum from which they are derived, and moved forward, sometimes even entirely fused with the sclerites anterior to them. These sclerites bearing the second and third phragmata are called postnota (Figures 2–6 and 2–7, PN$_2$, PN$_3$).

The lateral portion of the thorax in winged insects is very different from the abdomen in that typically it is strongly sclerotized and relatively rigid. The origin of these pleural sclerites has been considerably debated. Some researchers have argued that these pleural sclerites evolved *de novo* and have no serial homologs in other parts of the body. Many others postulate that the pleural sclerites represent the incorporation of a basal leg segment, the subcoxa, into the body wall. Finally, others have suggested that, in essence, both are correct in that the thoracic pleurites are composite in origin. In any case, the sclerotized portion of the pleuron is divided by a suture that extends from the base of the leg to the base of the wing; this is the **pleural suture** (Figure 2–6, pls). This suture divides the pleuron into an anterior episternum (Figure 2–6, eps$_1$–eps$_3$) and a posterior epimeron (Figure 2–6, epm$_1$–epm$_3$). According to the subcoxal theory of the origin of pleural sclerites, the pleurites originally consisted of a pair of incomplete rings above the base of the leg: an upper anapleurite and a lower catepleurite (the latter also called *katepleurite, catapleurite,* or *coxopleurite*). Such sclerites are visible in the primitively wingless hexapods and in a few pterygotes. The catepleurite articulates with the leg. Thus the combination of the pleural suture and the two rings of the subcoxa can theoretically define four regions of the pleuron: anepimeron, anepisternum, catepimeron, and catepisternum (for an example, see terminology of McAlpine et al. 1981 for the dipteran thorax in Chapter 33). In addition to its dorsal articulation with the catepleurite, the leg articulates anteroventrally with a narrow sclerite (often entirely fused with the episternum), the trochantin. The wing rests on the pleural wing process (Figure 2–6, pwp), which forms the dorsal apex of the pleural suture. Anterior to the pleural wing process is a small sclerite, the **basalare** (Figure 2–12A,B, ba); posterior to the pleural wing process is another sclerite, the **subalare** (Figure 2–12A, sb; occasionally two small sclerites are found here instead of one). These sclerites (sometimes collectively called *epipleurites*) are attached to the base of the wing and serve as means of controlling the attitude of the wings or may be directly involved in wing movement.

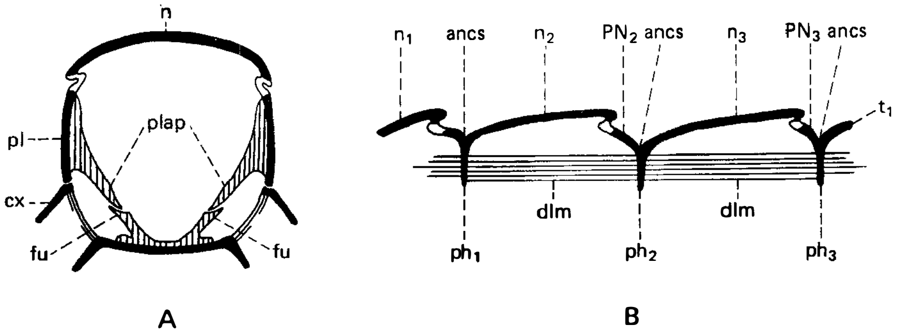

Figure 2–7 Endoskeleton of the thorax (diagrammatic). A, Cross section of a thoracic segment; B, Longitudinal section of the thoracic dorsum. *ancs*, antecostal suture; *cx*, coxa; *dlm*, dorsal longitudinal muscles; *fu*, sternal apophyses or furca; *n*, notum; *n$_1$*, pronotum; *n$_2$*, mesonotum; *n$_3$*, metanotum; *ph*, phragmata; *pl*, pleuron; *plap*, pleural apophyses; *PN$_2$*, mesopostnotum; *PN$_3$*, metapostnotum; *t$_1$*, first abdominal tergum. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

The external pleural suture corresponds to an internal costa, the pleural ridge. This ridge extends internally on either side as a pair of **pleural apophyses** (or pleural arms; Figure 2–7A, plap). These pleural apophyses are connected with a corresponding pair of apophyses arising from the sternum (Figure 2–7A, fu). The two may be connected by muscle or tendon, or in some cases they are fused together. The bases of the sternal apophyses are often fused together, particularly in species in which the legs are contiguous ventrally. The apophyses then have a Y-shaped appearance, and the structure is called the **furca**.

Legs

The thoracic legs of insects are sclerotized and subdivided into a number of segments. There are typically six segments (Figure 2–8): the coxa (cx), the basal segment; the **trochanter** (tr), a small segment (occasionally two segments) following the coxa; the **femur** (fm), usually the first long segment of the leg; the **tibia** (tb), the second long segment; the **tarsus** (ts), usually a series of small subdivisions beyond the tibia; and the **pretarsus** (ptar), consisting of the claws and various padlike or setalike structures at the apex of the tarsus. A **true segment** of an appendage (including the six just described) is a subdivision with musculature inserted at its base. The subdivisions of the tarsus, though commonly called *tarsal segments*, are not true segments in this sense and are more properly called *subsegments* or *tarsomeres*. The pretarsus usually includes one or more padlike structures between or at the base of the claws. A pad or lobe between the claws is usually called an **arolium** (Figure 2–8A,B, aro), and pads located at the base of the claws are usually called **pulvilli** (Figure 2–8C, pul).

The movements of a leg depend on its musculature and the nature of the joints between its segments. These leg joints may be **dicondylic**, with two points of articulation, or **monocondylic**, with a single point of articulation (Figure 2–9). The movement at a dicondylic joint is largely limited to the plane perpendicular to a line connecting the two points of articulation, whereas that at a

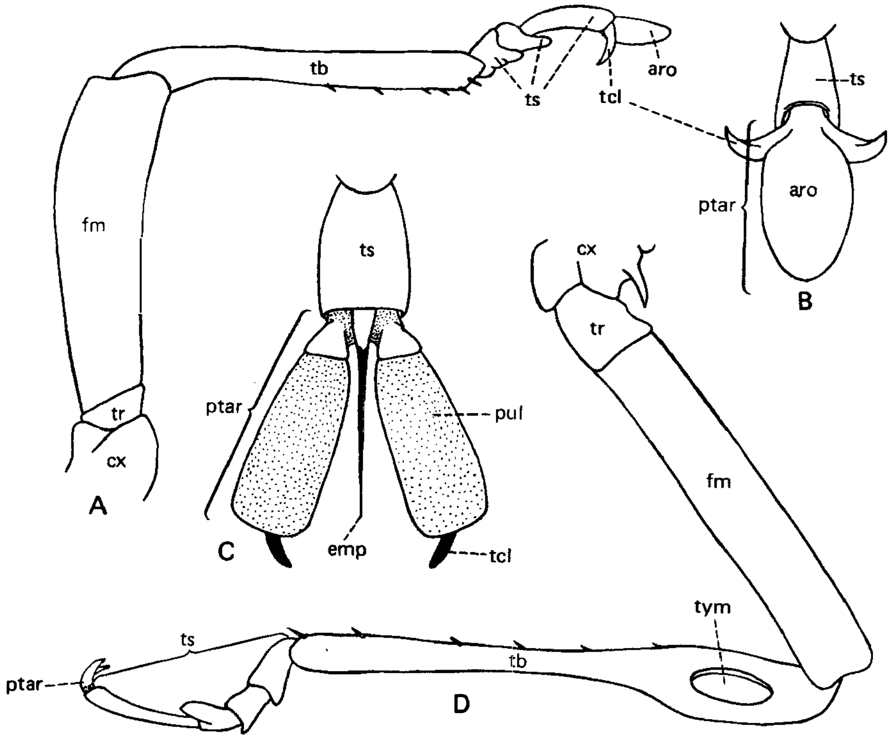

Figure 2–8 Leg structure in insects. A, Middle leg of a grasshopper (*Melanoplus*); B, Last tarsal segment and pretarsus of *Melanoplus*; C, Last tarsal segment and pretarsus of a robber fly; D, Front leg of a katydid (*Scudderia*). *aro*, arolium; *cx*, coxa; *emp*, empodium; *fm*, femur; *ptar*, pretarsus; *pul*, pulvillus; *tb*, tibia; *tcl*, tarsal claw; *tr*, trochanter; *ts*, tarsus; *tym*, tympanum.

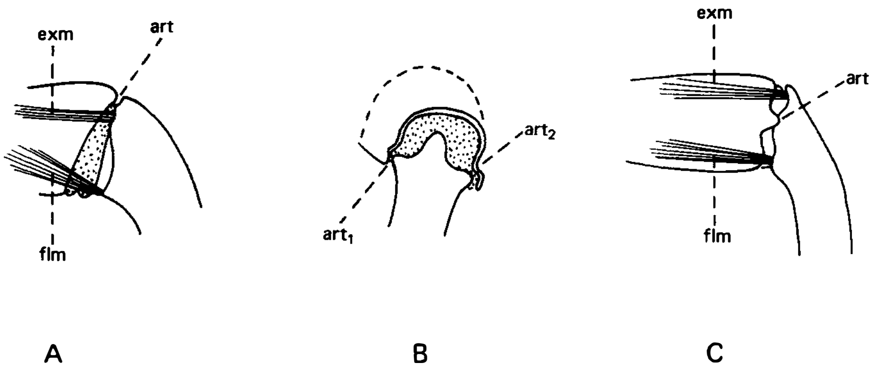

Figure 2–9 Articular mechanisms in insect legs. A, A monocondylic joint; B, C, End view and side view of a dicondylic joint. *art*, points of articulation; *exm*, extensor muscle; *flm*, flexor muscle. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

monocondylic joint (which is like a ball-and-socket joint) can be more varied. The joints between the coxa and body may be monocondylic. If it is dicondylic, the axis of rotation is usually more or less vertical, and the leg moves forward and backward (promotion and remotion). The coxo-trochanteral, trochantero-femoral, and femoro-tibial joints are usually dicondylic. The movement between the coxa and trochanter and the femur and tibia is dorsal and ventral (elevation and depression of the leg). The tibio-tarsal joint is usually monocondylic, thus permitting more varied movements.

Wings

The wings of insects are outgrowths of the body wall located dorsolaterally between the nota and pleura. They arise as saclike outgrowths, but when fully developed are flattened and flaplike, and are strengthened by a series of sclerotized veins. Among living insects, fully developed and functional wings are usually present only in the adult stage. The one exception is the presence of functional wings in the penultimate instar in Ephemeroptera (the subimago). At most, two pairs of wings are found in living insects, located on the mesothoracic and metathoracic segments. Most of the muscles that move the wings are attached to sclerites in the thoracic wall rather than to the wings directly, and the wing movements are produced indirectly by changes in the shape of the thorax.

The wing veins are hollow structures that may contain nerves, tracheae, and hemolymph (blood). The pattern of venation varies considerably among different groups of insects. Little is known about the functional significance of these differences, but the pattern of wing venation is very useful as a means of identification. Several venational terminologies have been developed, and the most widely used has been the Comstock-Needham system (Comstock and Needham 1898, 1899) (see Figure 2–10). This system basically recognizes a series of six major longitudinal wing veins (with their abbreviations in parentheses): **costa** (C) at the leading edge of the wing, followed by the **subcosta** (Sc), **radius** (R), **media** (M), **cubitus** (Cu), and **anal veins** (A). Each of these veins, with the exception of the costa, may be branched. The subcosta may branch once. The branches of the longitudinal veins are numbered from anterior to posterior around the wing by means of subscript numerals: the two branches of the subcosta are designated Sc_1 and Sc_2. The radius first gives off a posterior branch, the **radial sector** (Rs), usually near the base of the wing; the anterior branch of the radius is R_1; the radial sector may fork twice, with four branches reaching the wing margin. The media may fork twice, with four branches reaching the wing margin. The cubitus, according to the Comstock-Needham system, forks once, the two branches being Cu_1 and Cu_2; according to some other authorities, Cu_1 forks again distally, with the two branches being Cu_{1a} and Cu_{1b}. The anal veins are typically unbranched and are usually designated from anterior to posterior as the first anal vein (1A), second anal vein (2A), and so on.

Crossveins connect the major longitudinal veins and are usually named accordingly (for example, the medio-cubital crossvein, m-cu). Some crossveins have special names: two common examples are the **humeral crossvein** (h) and the **sectorial crossvein** (s).

The spaces in the wing membrane between the veins are called **cells**. Cells may be open (extending to

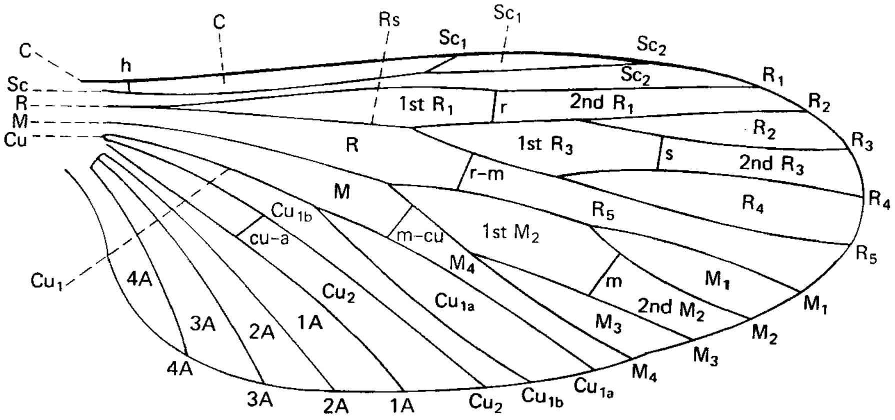

Figure 2–10 Generalized wing venation, according to Comstock; for a key to the lettering, see accompanying text. In some orders the vein here labeled Cu_1 is called Cu in the Comstock-Needham system (and its branches Cu_1 and Cu_2), and the remaining veins anal veins.

the wing margin) or closed (completely surrounded by veins). The cells are named according to the longitudinal vein on the anterior side of the cell; for example, the open cell between R_2 and R_3 is called the R_2 cell. Where two cells separated by a crossvein would ordinarily have the same name, they are individually designated by number; for example, the medial crossvein connects M_2 and M_3 and divides the M_2 cell into two cells, the basal one is designated the first M_2 cell and the distal one the second M_2 cell. Where a cell is bordered anteriorly by a fused vein (for example, R_{2+3}), it is named after the posterior component of that fused vein (cell R_3). In some insects, certain cells may have special names, for example, the triangles of the dragonfly wing and the discal cell of the Lepidoptera.

The wings of insects are attached to the thorax at three points (see Figures 2–11 and 2–12): with the notum at the **anterior and posterior notal wing processes** (Figure 2–11, awp, pnwp), and ventrally at the pleural wing process (Figure 2–12A, pwp). In addition, small sclerites, the axillary sclerites (or pteralia) at the base of the wing are important in translating the movements of the thoracic sclerites into wing movements. Most living insects (the Neoptera) have three axillary sclerites (Figure 2–11, axs_1–axs_3). Anteriorly the first axillary articulates with the anterior notal wing process,

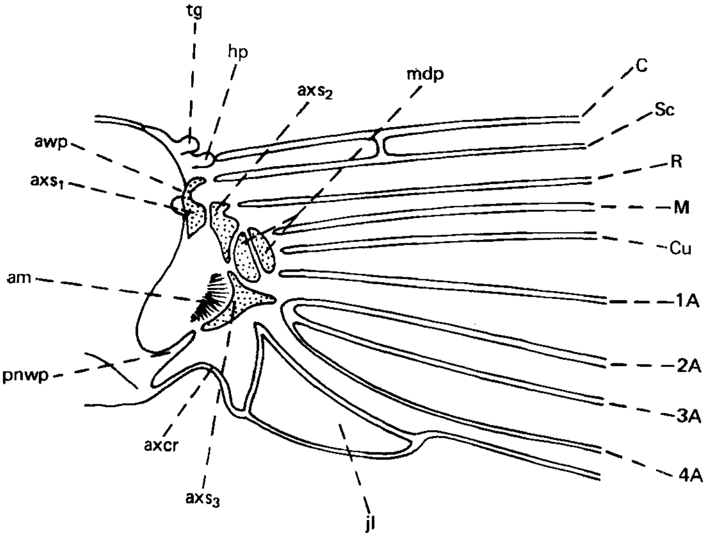

Figure 2–11 Diagram showing the articulation of the wing with the thoracic notum. *am*, axillary muscles; *awp*, anterior notal wing process; *axcr*, axillary cord; *axs*, axillary sclerites 1–3; *hp*, humeral plate; *jl*, jugal lobe; *mdp*, median plates; *n*, notum; *pnwp*, posterior notal wing process; *tg*, tegula. The letters at the right side of the figure indicate the veins. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

the subcostal vein, and the second axillary. The second axillary then articulates with the first, the radial vein, the pleural wing process, and the third axillary. The third axillary articulates with the second, the anal veins, and the posterior notal wing process. In the Neoptera, a muscle (am) inserted on the third axillary causes it to pivot about the posterior notal wing process and thereby to fold the wing over the back of the insect. (Some groups of Neoptera, such as butterflies, have lost this ability to flex the wings over the back.) Two groups of winged insects, the Ephemeroptera and Odonata, have not evolved this wing-flexing mechanism, and their axillary sclerites are arranged in a pattern different from that of the Neoptera. Some specialists classify these two orders (with a number of extinct orders) together as the Paleoptera.

The Comstock-Needham system made great strides in recognizing the homology in wing veins among the orders and in reducing the number of names associated with them. Kukalová-Peck (1978, 1983, 1985) and Riek and Kukalová-Peck (1984) have proposed a reinterpretation of the origin and basic structure of insect wings. The veins are interpreted to consist of a series of paired blood channels that loop from the base of the wing to the apex and back again. The anterior vein in the loop protrudes from the dorsal surface (a convex vein) and the posterior vein in the loop protrudes from the ventral surface (a concave vein). The fundamental venation in this interpretation consists of eight major longitudinal vein systems: the precosta, costa, subcosta, radius, media, cubitus, anal vein, and jugal vein. The "vein" in the costal margin of living insects is thus formed from the fusion of the precosta, costa, and sometimes portions of the subcosta. This interpretation has been applied to the orders Ephemeroptera and Odonata, cases in which peculiarities in venation and axillary structure had led some to postulate that wings had evolved in insects more than once (see Chapters 9 and 10).

Flight

Many insects have powers of flight that exceed those of all other flying animals; they can steer accurately and quickly, hover, and go sideways or backward. Only the hummingbirds rival insects in their ability to maneuver on the wing.

Most insects have two pairs of wings, and the two wings on each side may be overlapped at the base or hooked together in some way so that they move together as one, or they may be capable of independent movement. In many Odonata, the front and hind wings move independently, and there is a phase difference in the movements of the two pairs; that is, when one pair is moving up, the other pair is moving down. In other Odonata and in most Orthoptera, the phase difference is less pronounced, with the front wings moving a little ahead of the hind wings.

The forces needed to fly—lift, thrust, and attitude control—are generated by the movement of the wings through the air. These movements, in turn, are generated by the thoracic muscles pulling either directly on the base of the wing (direct flight mechanism) or causing changes in the shape of the thorax, which in turn are translated by the axillary sclerites into wing movements (indirect flight mechanism). In most insects, the primary flight muscles are indirect: the dorsal longitudinal muscles (Figure 2–12A,B, dlm) cause the notum to bow, thereby raising the notal wing processes in relation to the pleural wing process, depressing the wing. The antagonistic movement is generated by contracting the tergosternal (dorsoventral or tergopleural) (Figure 2–12B, tsm); these pull down on the notum, drawing the notal wing processes down in relation to the pleural wing process, thereby elevating the wing. In addition, muscles inserted on the basalare (Figure 2–12, bms) and subalare (Figure 2–12A, sbm) can be involved in direct depression of the wing (by means of their connection to the wing margin at x_1 and x_2) or may be important in controlling the angle at which the wing moves through the air.

Flight, however, is not a simple matter of flapping the wings up and down. In addition, the wings are brought forward (promotion) and backward (remotion), and twisted; that is, the leading edge is turned downward (pronation) or the trailing edge is turned downward (supination). The manner in which these wing movements are produced involves a complex integration of the anatomical details of the attachment of the wing to the thorax and the contraction of muscles. The details are not completely known for any species, and only in a few can we begin to say we understand them at all. In fact, it is clear that insects of different sizes and shapes fly in different ways. A minute parasitic wasp of about 1 mm in length moves its wings differently and has wings of a different shape from a house fly's, for example, and the aerodynamics of its flight are probably also quite different.

Head

The head of insects consists of a series of metameric body segments, together specialized for food gathering and manipulation, sensory perception, and neural integration. Exactly how many segments are in the head has long been a matter of contention among morphologists, with the postulated number ranging from 3 to 7. The head bears the eyes, antennae, and mouthparts. Its

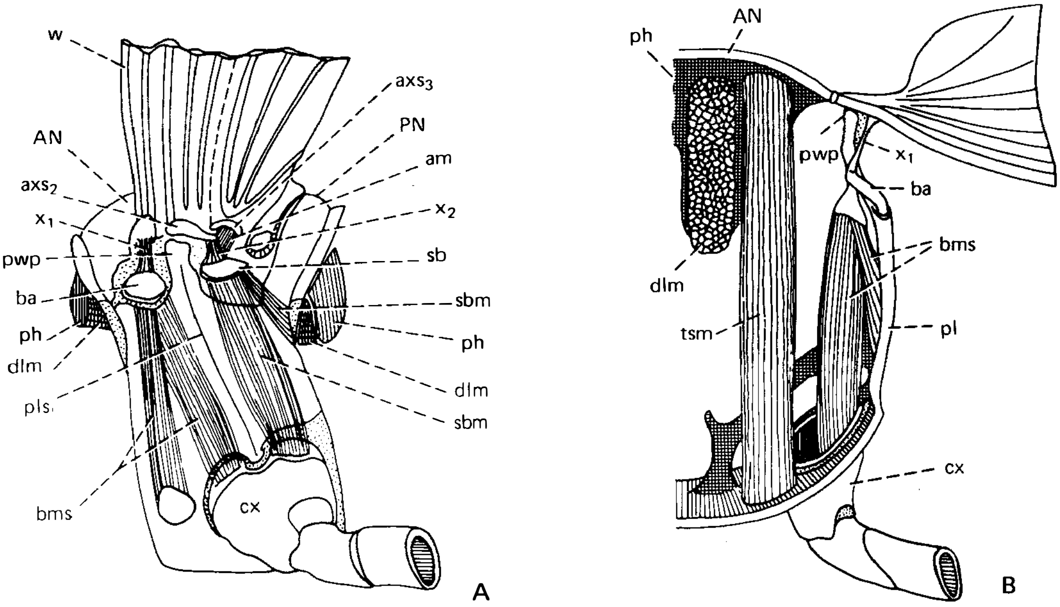

Figure 2–12 Diagram of the wing muscles of an insect. A, Lateral view; B, Cross section of a wing-bearing segment. *am*, axillary muscles; *AN*, alinotum; *axs*$_2$ and *axs*$_3$, second and third axillary sclerites; *ba*, basalare; *bms*, basalar muscles; *cx*, coxa; *dlm*, dorsal longitudinal muscles; *ph*, phragma; *pl*, pleuron; *pls*, pleural suture; *PN*, postnotum; *pwp*, pleural wing process; *sb*, subalare; *sbm*, subalar muscles; *tsm*, tergosternal muscles; *w*, wing; x_1 and x_2, connections between basalare and subalare and wing base. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

shape differs quite widely between groups of insects, but some landmarks are consistently visible to enable identification of its component parts.

The head is divided by grooves into a number of more or less distinct sclerites (Figure 2–13). Typically there is a transverse sulcus extending across the lower part of the face just above the base of the mouthparts; the medial or anterior part of this sulcus is the epistomal sulcus (es), and the lateral portions above the mandibles and maxillae are the **subgenal sulci** (sgs). The anterior portion of the head capsule, above the epistomal sulcus and between the large compound eyes, is the **frons** (fr). The anterior area below the epistomal sulcus is the **clypeus** (clp). The area below the eye, on the side of the head, and above the subgenal sulcus is the gena (ge). The top of the head, between the eyes, is the vertex (ver). In many, if not most insects, the frons, vertex, and genae are general areas of the head, and their edges are not clearly defined by sulci.

The head is connected to the thorax by the membranous cervix (cvx). The opening on the posterior side of the head is the **occipital** foramen (or foramen magnum; for); through it run the ventral nerve cord, tracheae, the digestive system, muscles, sometimes the dorsal blood vessel, and so on. The most posterior line of inflection on the head capsule outside of the occipital foramen is generally the **postoccipital** suture (pos). This suture defines the limits of the posterior segment of the head, the labial segment, named because it bears ventrally the most posterior set of mouthparts, the labium. The area behind the postoccipital suture is the **postocciput** (po); the area on the side of the head anterior to this suture is the postgena (pg); and the dorsal portion of the head anterior to the suture is the **occiput** (ocp). In some cases an **occipital sulcus** (os) is present that defines the anterior limits of the occiput and postgenae (separating them from the vertex and genae), but this is far from universally present.

The points on the head where the arms of the **tentorium** (a set of internal braces, see later) meet the head wall are usually marked by pits or slits visible externally. The anterior **tentorial pits** (atp) are at the lateral ends of the epistomal sulcus; the **posterior tentorial pits** (ptp) are at the lower ends of the postoccipital suture.

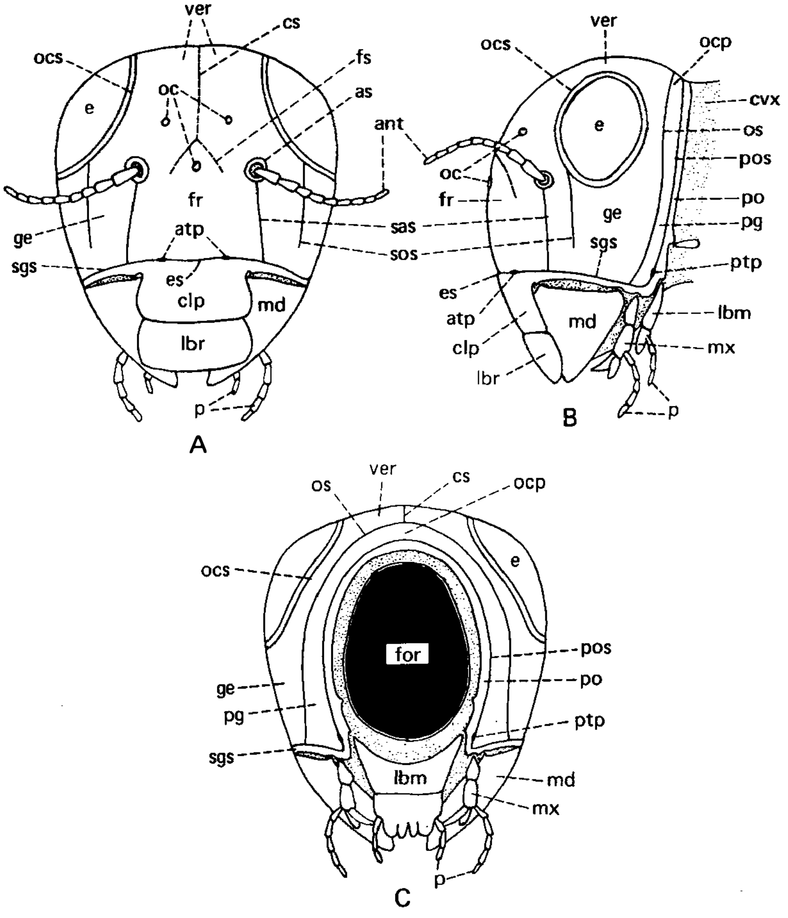

Figure 2–13 General structure of an insect head. A, Anterior view; B, Lateral view; C, Posterior view. *ant*, antenna; *as*, antennal sulcus; *atp*, anterior tentorial pit; *clp*, clypeus; *cs*, coronal suture; *cvx*, cervix; *e*, compound eye; *es*, epistomal sulcus; *for*, foramen magnum; *fr*, frons; *fs*, frontal suture; *ge*, gena; *lbm*, labium; *lbr*, labrum; *md*, mandible; *mx*, maxilla; *oc*, ocelli; *ocp*, occiput; *ocs*, ocular sulcus; *os*, occipital sulcus; *p*, palps; *pg*, postgena; *po*, postocciput; *pos*, postoccipital suture; *ptp*, posterior tentorial pit; *sas*, subantennal sulcus; *sgs*, subgenal sulcus; *sos*, subocular sulcus; *ver*, vertex. (Modified from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

In different insect groups the sulci and sclerites just described may be absent, or they may be supplemented by others. The nomenclature usually makes use of the landmarks mentioned; for example, the frontogenal sulci are lines of inflection separating the genae from the frons. In many groups, however, the naming of these parts follows the traditions taxonomists developed over the last century or more, and may not be standardized.

The head is braced internally by a group of apophyses forming the tentorium (Figure 2–14). This structure is usually H-shaped, X-shaped, or shaped like the Greek letter π (pi) with the principal arms in a more or less horizontal plane and extending from the lower part of the rear of the head to the face. The points where the anterior arms of the tentorium (Figure 2–14, ata) meet the face are marked externally by the anterior tentorial pits (atp), which are located at either end of the epistomal sulcus between the frons and the clypeus. The posterior arms of the tentorium meet the head wall at the posterior tentorial pits (ptp), which are located at the lower ends of the postoccipital sutures. These arms unite from side to side to form a tentorial bridge (Figure 2–14, ttb). Some insects have dorsal arms on the tentorium (dta) that extend to the upper part of the face near the antennal bases. The tentorium serves to brace the head capsule against the pull of the powerful mandibular muscles, as the point of attachment for muscles moving the head appendages, and as protection for the subesophageal ganglion and pharynx.

The head appendages of hexapods, starting posteriorly and moving forward, are (1) the **labium** (Figure 2–13, lbm); (2) the **maxillae** (mx); (3) the **mandibles** (md); (4) the **labrum** (lbr); and (5) the **antennae** (ant). These are described in more detail later. These represent modified appendages, serially homologous to the thoracic walking legs. In the ancestral condition, the mouthparts are directed downward; such a head is called **hypognathous**. In many predatory and burrowing species, the mouthparts are directed anteriorly, the **prognathous** condition. Finally, in some groups, espe-

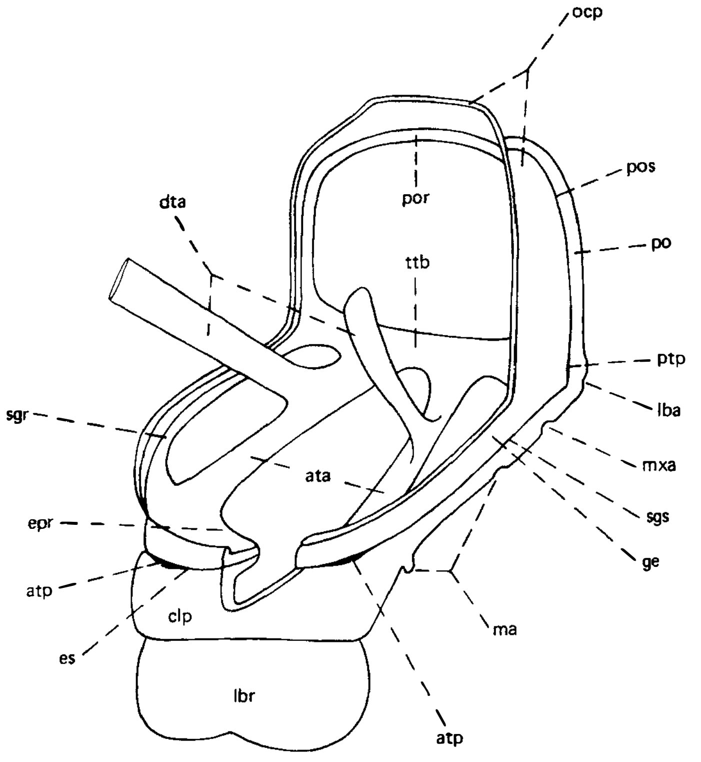

Figure 2–14 Head of an insect with a section of the head wall cut away to show the tentorium (diagrammatic). *ata*, anterior tentorial arms; *atp*, anterior tentorial pits; *clp*, clypeus; *dta*, dorsal tentorial arms; *epr*, epistomal ridge; *es*, epistomal sulcus; *ge*, gena; *lba*, labial articulation; *lbr*, labrum; *ma*, mandibular articulation; *mxa*, maxillary articulation; *ocp*, occiput; *po*, postocciput; *por*, postoccipital ridge; *pos*, postoccipital suture; *ptp*, posterior tentorial pit; *sgr*, subgenal ridge; *sgs*, subgenal sulcus; *ttb*, tentorial bridge. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

cially the Hemiptera, the mouthparts are directed posteriorly; this is the **opisthognathous** condition (or, when speaking of the beak of Hemiptera, the opisthorhynchous condition).

The posterior surface of the head, between the foramen and the labium, is membranous in most insects, but in a few this region is sclerotized. This sclerotization may be the result of the hypostomal areas (areas below the subgenal sulci posterior to the mandibles) extending ventrally and toward the midline to form what is called a **hypostomal bridge**, or (particularly in prognathous insects) the result of the postoccipital sutures extending forward onto the ventral side of the head, with a sclerite developing between these sutures and the foramen. In the latter case the sclerite is called the gula (see Figure 26-4, gu) and the anterior extensions of the postoccipital sutures are called **gular** sutures. In some groups, the hypostomal bridge may be "overgrown" by extensions of the postgenae, thus creating a postgenal **bridge**.

The number of segments making up the head is not apparent in the adult insect, as the head sulci rarely coinicide with the sutures between the original segments. Entomologists do not agree on the number of segments in the insect head; the one area of consensus is that the posterior three sets of mouthparts correspond to appendages (serially homologous with the thoracic legs) of three postoral (behind the mouth) segments. The area anterior to the mouth bears the compound eyes, ocelli, antennae, and labrum; the interpretation of this region is a matter of contention, and some of the hypotheses and the evidence in support of them are succinctly summarized by Rempel (1975). Recent developmental and molecular studies support the idea that both the labrum and antennae are modified appendages associated with independent head segments.

Antennae

The antennae are paired segmented appendages located on the head, usually between or below the compound eyes. The basal segment is called the scape (Figure 2–15N, scp), the second segment the **pedicel** (ped), and the remainder the **flagellum** (fl). In insects (the Pterygota and the apterous orders Thysanura and Microcoryphia), the "segments" of the flagellum lack intrinsic musculature and therefore are thought to represent subsegments of the apical, third true antennal segment. These are often called *flagellomeres* to distinguish them from true musculated segments (although this anatomical characteristic is widely recognized, these subsegments are still often called *segments*). This type of antenna is called an annulated antenna, refer-

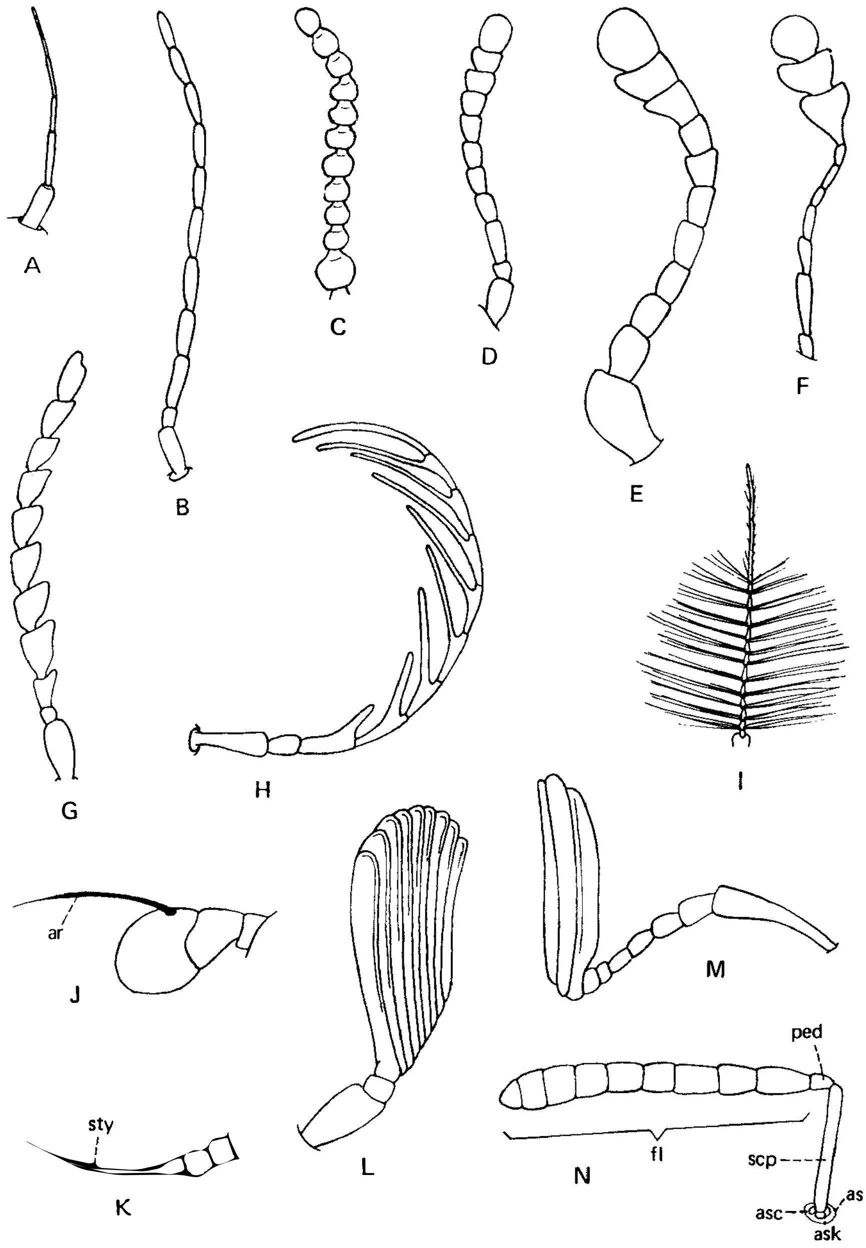

Figure 2–15 Types of antennae. A, Setaceous (dragonfly); B, Filiform (ground beetle); C, Moniliform (wrinkled bark beetle); D, Clavate (darkling beetle); E, Clavate (ladybird beetle); F, Capitate (sap beetle); G, Serrate (click beetle); H, Pectinate (fire-colored beetle); I, Plumose (male mosquito); J, Aristate (syrphid fly); K, Stylate (snipe fly); L, Flabellate (cedar beetle); M, Lamellate (June beetle); N, Geniculate (chalcid). Antennae such as those in D–F, L, and M are also called clubbed. *ar*, arista; *as*, antennal sulcus; *asc*, antennal sclerite; *ask*, antennal socket; *fl*, flagellum; *ped*, pedicel; *scp*, scape; *sty*, style.

ring to the subsegmentation of the flagellum. In the orders Diplura and Collembola, more than the basal three antennal segments are musculated; these are called segmented antennae. An antenna arises from an antennal socket that is membranous but is surrounded by a ringlike antennal sclerite that often bears a small process, the antennifer, on which the scape pivots. The antennae are primarily sensory in function and act as tactile organs, organs of smell, and in some cases organs of hearing.

Insect antennae vary greatly in size and form and are important in identification. The following terms are used to describe their shapes:

Setaceous—bristlelike, the segments becoming more slender distally; for example, dragonfly (Figure 2–15A), damselfly, leafhopper.

Filiform—threadlike, the segments nearly uniform in size and usually cylindrical; for example, ground beetle (Figure 2–15B), tiger beetle.

Moniliform—like a string of beads, the segments similar in size and more or less spherical in shape; for example, wrinkled bark beetle (Figure 2–15C).

Serrate—sawlike, the segments, particularly those in the distal half or two thirds of the antenna, more or less triangular; for example, click beetle (Figure 2–15G).

Pectinate—comblike, most segments with long, slender, lateral processes; for example, fire-colored beetle (Figure 2–15H).

Clubbed—the segments increasing in diameter distally (Figure 2–15D-F,L,M). If the increase is gradual, the condition may be termed clavate (Figure 2–15D,E). This name is also used more or less synonymously with the term *clubbed*. If the terminal segments are rather suddenly enlarged, the condition is termed capitate (Figure 2–15F). If the terminal segments are expanded laterally to form rounded or oval platelike lobes, the condition is termed lamellate (Figure 2–15M). Where the terminal segments have long, parallel-sided, sheetlike, or tonguelike lobes extending laterally, the condition is termed flabellate (Figure 2–15L).

Geniculate—elbowed, with the first segment long and the following segments small and arising at an angle to the first; for example, stag beetle, ant, chalcid (Figure 2–15N).

Plumose—feathery, most segments with whorls of long hair; for example, male mosquito (Figure 2–15I).

Aristate—the last segment usually enlarged and bearing a conspicuous dorsal bristle, the arista; for example, housefly, syrphid fly (Figure 2–15J).

Stylate—the last segment bearing an elongate terminal stylelike or fingerlike process, the style; for example, robber fly, snipe fly (Figure 2–15K).

Mouthparts

Insect mouthparts typically consist of a labrum, a pair each of mandibles and maxillae, a labium, and a hypopharynx. These structures are modified, sometimes significantly, in different insect groups and are often used in classification and identification. The type of mouthparts an insect has determines how it feeds and (in the case of most injurious species) what sort of damage it does. We describe next the basic structure of the mouthparts, followed by a few of the significant modifications. Further information on the variations in mouthpart structure can be found in the discussion of individual insect orders.

Mandibulate Mouthparts

The most generalized condition of the mouthparts is found in chewing insects, such as a cricket. These are said to be "chewing" or "mandibulate" mouthparts because of the heavily sclerotized mandibles that move transversely and are able to bite off and chew particles of food. You can most easily see and study the mouthparts by removing them from a preserved specimen one at a time and examining them under a microscope.

The labrum, or upper lip (Figure 2–13, lbr; Figure 2–16E), is a broad, flaplike lobe located below the clypeus on the anterior side of the head, in front of the other mouthparts. On the posterior or ventral side of the labrum may be a swollen area, the epipharynx.

The mandibles (Figure 2–13, md; Figure 2–16D) are the paired, heavily sclerotized, unsegmented jaws lying immediately behind the labrum. In the winged insects and the order Thysanura, they articulate with the head capsule at two points, one anterior and one posterior, and move transversely (and therefore these two taxa are classified together as the Dicondylia). The mandibles of chewing insects may vary somewhat in structure; in some insects (including the cricket), they bear both cutting and grinding ridges, whereas in others (such as certain predaceous beetles) they are long and sicklelike.

The maxillae (Figure 2–13, mx; Figure 2–16A) are paired structures lying behind the mandibles; they are segmented, and each maxilla bears a feelerlike organ, the maxillary palp (mxp). The basal segment of the maxilla is the cardo (cd, plural *cardines*); the second segment is the stipes (stp, plural *stipites*). The palp is borne on a lobe of the stipes called the palpifer (plf). The stipes bears at its apex two processes: the lacinia (lc), an elongate jawlike structure; and the galea (g), a lobelike structure.

The labium, or lower lip (Figure 2–13, lbm; Figure 2–16C), is a single median structure (although it is derived from two maxilla-like mouthparts fusing along the midline) lying behind the maxillae. It is divided by a transverse sulcus into two portions, a basal

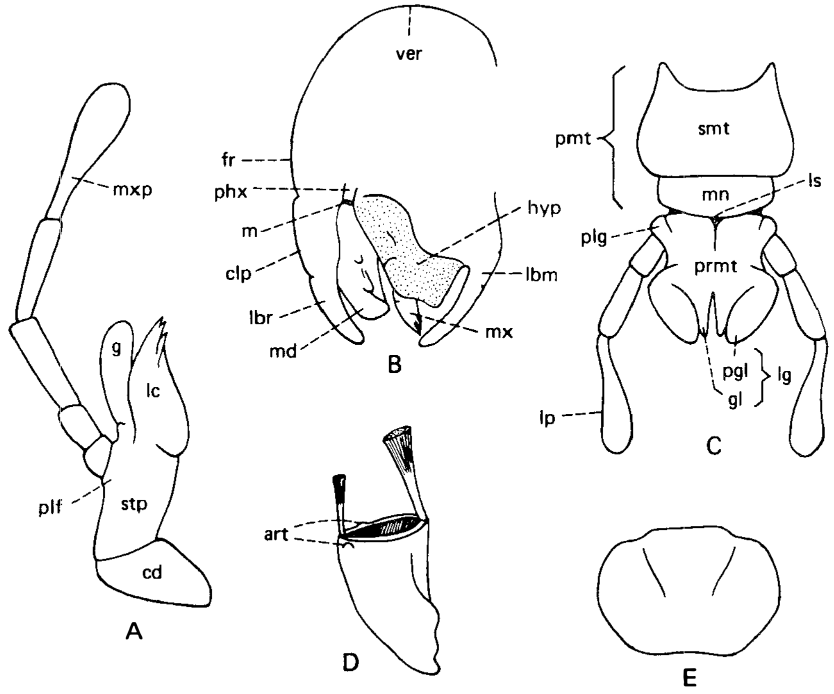

Figure 2–16 Mouthparts of a cricket (*Gryllus*). A, Maxilla; B, Median vertical section of the head, showing relation of hypopharynx (*hyp*) to the other parts (somewhat diagrammatic); C, Labium; D, Mandible, showing muscle attachments and points of articulation; E, Labrum. *art*, points of articulation of mandible; *cd*, cardo; *clp*, clypeus; *fr*, frons; *g*, galea; *gl*, glossa; *hyp*, hypopharynx; *lbm*, labium; *lbr*, labrum; *lc*, lacinia; *lg*, ligula; *lp*, labial palp; *ls*, labial suture; *m*, mouth; *md*, mandible; *mn*, mentum; *mx*, maxilla; *mxp*, maxillary palp; *pgl*, paraglossa; *phx*, pharynx; *plf*, palpifer; *plg*, palpiger; *pmt*, postmentum; *prmt*, prementum; *smt*, submentum; *stp*, stipes; *ver*, vertex.

postmentum (pmt) and a distal **prementum** (prmt). The postmentum may be divided into a basal submentum (smt) and a distal mentum (mn). The prementum bears a pair of **labial palps** (lp) and a group of apical lobes that constitute the **ligula** (lg). The labial palps are borne on lateral lobes of the prementum, called **palpigers** (plg). The ligula consists of a pair of mesal lobes, the glossae (gl), and a pair of lateral lobes, the paraglossae (pgl).

If the mandible and maxilla on one side of a specimen are removed, the **hypopharynx** (Figure 2–16B, hyp) becomes visible; this is a short, tonguelike structure located immediately in front of or above the labium and between the maxillae. In most insects, the ducts from the salivary glands open on or near the hypopharynx. Between the hypopharynx, mandibles, and labrum lies the preoral food cavity, the **cibarium**, which leads dorsally to the mouth.

Variations in Insect Mouthparts

Insect mouthparts can be classified into two general types, mandibulate (chewing) and haustellate (sucking). In mandibulate mouthparts, the mandibles move transversely, that is, from side to side, and the insect is usually able to bite off and chew its food. Insects with haustellate mouthparts do not have mandibles of this type and cannot chew food. Their mouthparts are in the form of a somewhat elongated proboscis or beak through which liquid food is sucked. The mandibles in haustellate mouthparts either are elongate and styletlike or are lacking.

The Mouthparts of Hemiptera. The beak in this order (Figure 2–17) is elongate, usually segmented, and arises from the front (Heteroptera) or rear (Auchenorrhyncha, Sternorrhyncha) of the head. The external segmented structure of the beak is the labium which is sheathlike and encloses four piercing stylets: the two mandibles and the two maxillae. The labrum is a short lobe at the base of the beak on the anterior side, and the hypopharynx is a short lobe within the base of the beak. The labium does no piercing, but folds up as the stylets enter the tissue fed on. The inner stylets in the beak, the maxillae, fit together in such a way as to form two channels, a food channel and a salivary channel. The palps are lacking.

The Mouthparts of the Diptera. The biting Diptera in the suborder Nematocera and the Tabanomorpha include the mosquitoes (Figure 2–18), sand flies, punkies, black flies, horse flies, and snipe flies. Females of these insects have six piercing stylets: the labrum, the mandibles, the maxillae, and the hypopharynx; the labium usually serves as a sheath for the stylets. The stylets may be very slender and needlelike (mosquitoes) or broader and knifelike (the other groups). The maxillary palps are well developed, but labial palps are lacking (some dipterists regard the labellar lobes as

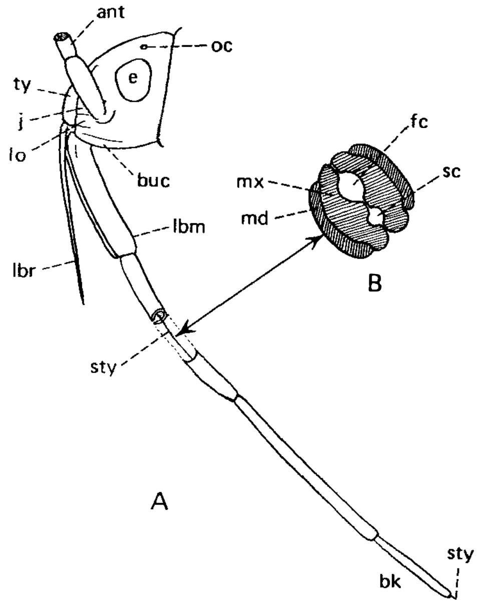

Figure 2–17 Mouthparts of the large milkweed bug, *Oncopeltus fasciatus* (Dallas). A, Lateral view of the head showing beak, with the labrum detched from front of beak; B, Cross section of stylets (somewhat diagrammatic). *ant*, antenna; *bk*, beak; *buc*, buccula; *e*, compound eye; *fc*, food channel; *j*, jugum; *lbm*, labium; *lbr*, labrum; *lo*, lorum; *md*, mandible; *mx*, maxilla; *oc*, ocellus; *sc*, salivary channel; *sty*, stylets; *ty*, tylus.

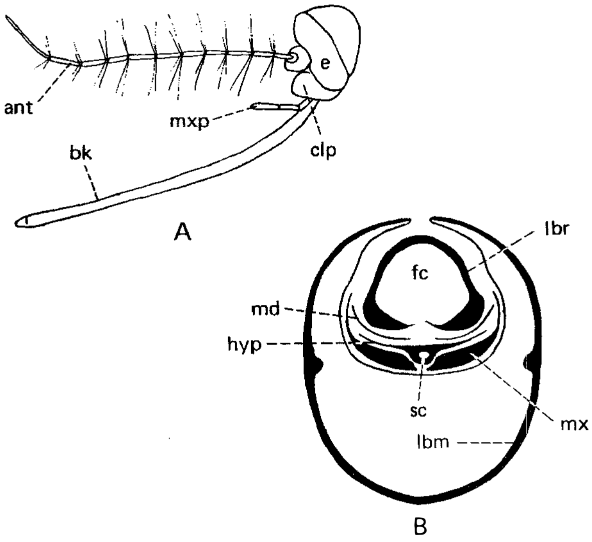

Figure 2–18 Mouthparts of a mosquito. A, Head of *Aedes*, lateral view; B, Cross section of proboscis of *Anopheles*. *ant*, antenna; *bk*, proboscis; *clp*, clypeus; *e*, compound eye; *fc*, food channel; *hyp*, hypopharynx; *lbm*, labium; *lbr*, labrum; *md*, mandible; *mx*, maxilla; *mxp*, maxillary palp; *sc*, salivary channel. (B, Redrawn from Snodgrass, after Vogel 1921.)

labial palps). The salivary channel is in the hypopharynx, and the food channel is located between the grooved labrum and the hypopharynx (for example, the mosquitoes) or between the labrum and the mandibles (for example, punkies and horse flies). The labium does no piercing and folds up or back as the stylets enter the tissue pierced.

The Muscomorpha lack mandibles, and the maxillae are represented by the palps (maxillary stylets are usually lacking). The proboscis consists of the labrum, hypopharynx, and labium. There are two modifications of the mouthparts in these flies: (a) a piercing type and (b) a sponging or lapping type.

The Muscomorpha with piercing mouthparts include the stable fly (Figure 2–19), tsetse fly, horn fly, and louse flies. The principal piercing structure in these flies is the labium; the labrum and hypopharynx are slender and styletlike and lie in a dorsal groove of the labium. The labium terminates in a pair of small, hard plates, the labella, which are armed with teeth. The salivary channel is in the hypopharynx, and the food channel is between the labrum and hypopharynx.

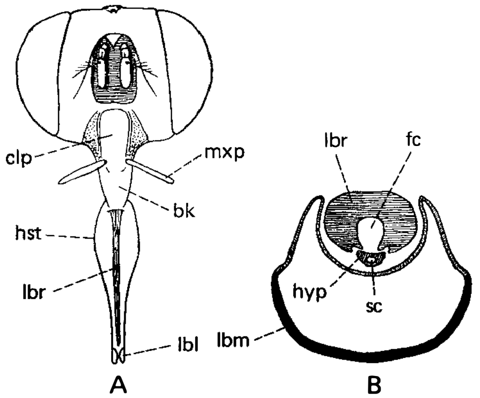

Figure 2–19 Mouthparts of the stable fly, *Stomoxys calcitrans* (L.). A, Anterior view of head; B, Cross section through haustellum. *bk*, rostrum; *clp*, clypeus; *fc*, food channel; *hst*, haustellum; *hyp*, hypopharynx; *lbl*, labellum; *lbm*, labium; *lbr*, labrum; *mxp*, maxillary palp; *sc*, salivary channel. (Redrawn from various sources; somewhat diagrammatic.)

The proboscis in the louse flies (Hippoboscidae) is somewhat retracted into a pouch on the ventral side of the head when not in use.

The remaining Diptera with sponging or lapping mouthparts include the nonbiting species such as the house fly (Figure 2–20), blow flies, and fruit flies. The mouthpart structures are suspended from a conical membranous projection of the lower part of the head called the *rostrum*. The maxillary palps arise at the distal end of the rostrum, and the part of the proboscis beyond the palps is termed the *haustellum*. The labrum and hypopharynx are slender and lie in an anterior groove of the labium, which forms the bulk of the haustellum. The salivary channel is in the hypopharynx, and the food channel lies between the labrum and the hypopharynx. At the apex of the labium are the labella, a pair of large, soft, oval lobes. The lower surface of these lobes bears numerous transverse grooves that serve as food channels. The proboscis can usually be folded up against the lower side of the head or into a cavity there. These flies lap up liquids; the food may be already in liquid form, or it may first be liquefied by salivary secretions of the fly.

The Mouthparts of Lepidoptera. The proboscis of adult Lepidoptera (Figure 2–21) is usually long and coiled and is formed of the two galeae of the maxillae; the food channel is between the galeae. The labrum is a narrow transverse band across the lower margin of the face, and there are no mandibles and hypopharynx (except in the Micropterigidae). The maxillary palps are usually small or absent, but the labial palps are usually well devel-

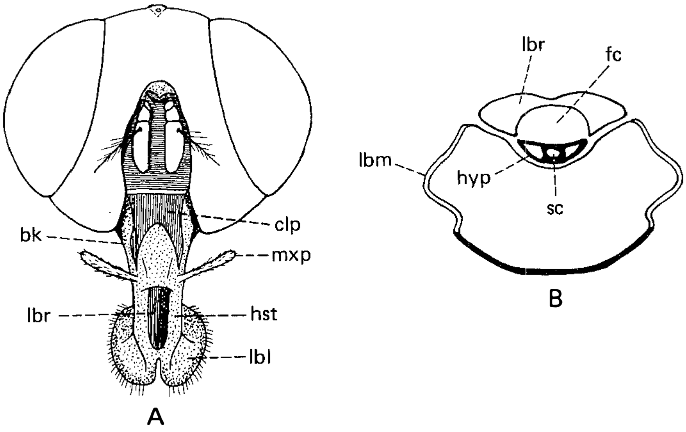

Figure 2–20 Mouthparts of the house fly, *Musca domestica* L. A, Anterior view of head; B, Cross section through haustellum. *bk*, rostrum; *clp*, clypeus; *fc*, food channel; *hst*, haustellum; *hyp*, hypopharynx; *lbl*, labellum; *lbm*, labium; *lbr*, labrum; *mxp*, maxillary palp; *sc*, salivary channel. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

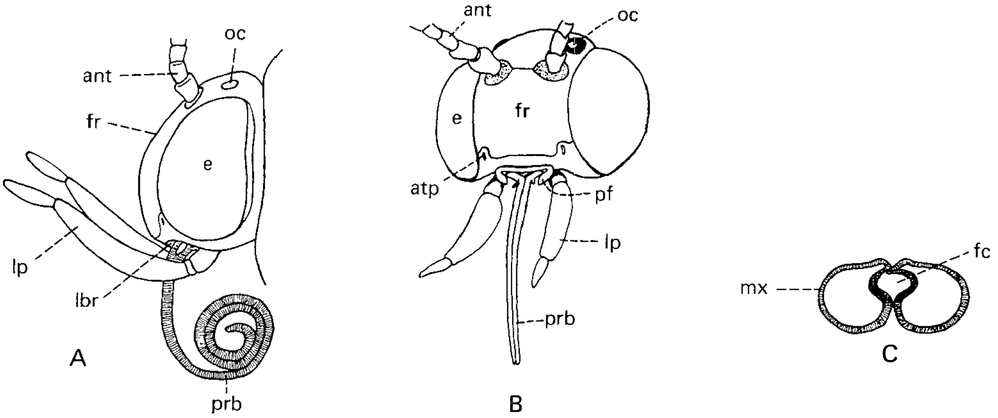

Figure 2–21 Mouthparts of a moth. A, Lateral view of head; B, Anterior view of head; C, Cross section through proboscis. *ant*, antenna; *atp*, anterior tentorial pit; *e*, compound eye; *fc*, food channel; *fr*, frons; *lbr*, labrum; *lp*, labial palp; *mx*, maxilla (galea); *oc*, ocellus; *pf*, pilifer; *prb*, proboscis. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

oped. There is no special salivary channel. This type of mouthpart structure is sometimes called *siphoning-sucking*, because there is usually no piercing and the insect merely sucks or siphons liquids up through the proboscis. Some moths in Southeast Asia and northern Australia, however, use the proboscis to pierce the skins of soft fruits and then siphon liquids from the tissues underneath. When used, the proboscis is uncoiled by blood pressure; it recoils by its own elasticity.

Insect Muscles

The muscular system of an insect is comprised of from several hundred to a few thousand individual muscles. All consist of striated muscle cells, even those around the alimentary canal and the heart. The skeletal muscles, which attach to the body wall, move the various parts of the body, including the appendages. The cell membranes of the muscle and epidermis are interdigitated and interconnected by desmosomes; from the desmosomes, microtubules run to the outer epidermal cell membrane, and from there attachment fibers run through the cuticle to the epicuticle. The attachment fibers are not broken down between the times when the epidermis is separated from the old cuticle (apolysis) and the shedding of that cuticle (ecdysis; see section on molting later). Thus the muscles remain attached to the body wall, and the insect continues to be able to move during the period when a new cuticle is being formed. The locations of the points of attachment of the skeletal muscles are sometimes useful in determining the homologies of various body parts. The visceral muscles, which surround the heart, the alimentary canal, and the ducts of the reproductive system, produce the peristaltic movements that move materials along these tracts. They usually consist of longitudinal and circular muscle fibers.

The muscles moving the appendages are arranged segmentally, generally in antagonistic pairs. Some appendage parts (for example, the galea and lacinia of the maxillae and the pretarsus) have only flexor muscles. These structures are usually extended by a combination of hemolymph pressure and the elasticity of the cuticle. Each segment of an appendage normally has its own muscles. The tarsal and flagellar "segments" do not have their own muscles and thus are not true segments.

Insect muscles seem to us to be very strong: Many insects can lift 20 or more times their body weight, and jumping insects can often jump distances equal to many times their own length. These feats appear very remarkable when compared to what humans can do; they are possible not because the muscles of insects are inherently stronger, but because insects are smaller. The power of a muscle varies with the size of its cross-sectional area, or with the square of its width; what the muscle moves (the mass of the body) varies with the cube of the linear dimension. Thus as the body becomes smaller, the muscles become relatively more powerful.

Insect muscles are often capable of extremely rapid contraction. Wing stroke rates of a few hundred per second are fairly common in insects, and rates up to 1000 or more per second are known. In insects with relatively slow wing-stroke rates and in most other skeletal muscles, each muscle contraction is initiated by a nerve impulse. Such muscles are called *synchronous* or *neurogenic muscles* because of this one-to-one correspondence between action potentials and muscle contractions. In insects with higher wing-beat frequencies, the muscles contract much more often than the rate at which neural impulses reach them. The rates of contraction in such asynchronous muscles (found principally in flight muscles but sometimes in other oscillating systems) depend on the characteristics of the muscles themselves and the associated sclerites. Nerve impulses are necessary to initiate contractions, but thereafter serve to generally maintain the rate of contractions rather than to stimulate each one individually.

That insect muscles may have such an extremely rapid contraction frequency, which is sometimes maintained for a prolonged period, attests to the efficiency of their metabolism. The tracheal system provides the large volumes of oxygen needed for such metabolic rates. In most insects, the tracheoles (across whose walls gas exchange takes place) indent the cell membranes of the muscles, thus minimizing the distance across which diffusion of gases must take place. Insects use a variety of fuels for flight. Carbohydrates are important for many species; in others, lipids are the primary fuels; in some flies (such as the tsetse), amino acids form the substrate for generating the energy necessary for flight.

Digestive System

Insects feed on almost every organic substance found in nature, and their digestive systems exhibit considerable variation. The alimentary canal is a tube, usually somewhat coiled, which extends from the mouth to the anus (Figure 2–22). It is differentiated into three main regions: the **foregut**, or stomodaeum; the **midgut**, or mesenteron; and the **hindgut**, or proctodaeum. Both the foregut and hindgut are derived from ectodermal tissue and are lined internally by a thin layer of cuticle, the **intima**. This cuticle is shed at each molt along with the outer exoskeleton.

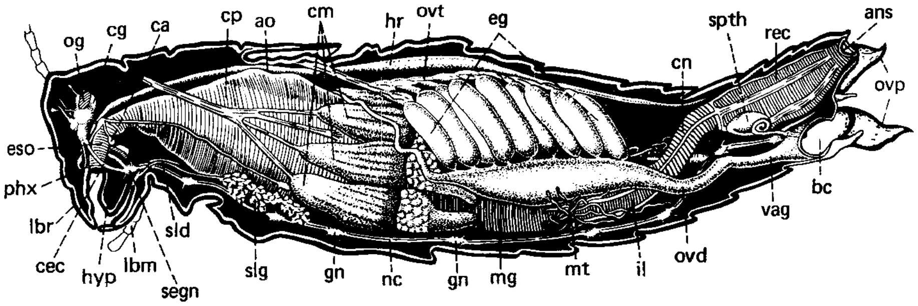

Figure 2–22 Internal organs of a grasshopper, shown in longitudinal section (somewhat diagrammatic). *ans*, anus; *ao*, dorsal aorta; *bc*, bursa copulatrix; *ca*, corpus allatum; *cec*, circumesophageal connective; *cg*, cerebral ganglion (part of the brain); *cm*, gastric caeca; *cn*, colon; *cp*, crop; *eg*, eggs; *eso*, esophagus; *gn*, ganglia of ventral nerve cord; *hr*, heart; *hyp*, hypopharynx; *il*, ileum; *lbm*, labium; *lbr*, labrum; *mg*, midgut or mesenteron; *mt*, Malpighian tubules; *nc*, ventral nerve cord; *og*, optic ganglion (part of the brain); *ovd*, oviduct; *ovp*, ovipositor; *ovt*, ovarian tubules; *phx*, pharynx; *rec*, rectum; *segn*, subesophageal ganglion; *slg*, salivary gland; *sld*, salivary duct; *spth*, spermatheca; *vag*, vagina. (Redrawn from Robert Matheson: *Entomology for Introductory Courses, Second Edition*. Comstock Publishing Company, Inc.)

Most insects have a pair of glands lying below the anterior part of the alimentary canal (Figure 2–22, slg). The ducts from these glands extend forward and unite into a common duct that opens near the base of the labium or hypopharynx. These **labial glands** (so named because they open at the base of the labium) generally function as salivary glands. There is often an enlargement of the duct from each gland that serves as a reservoir for the salivary secretion. The labial glands in the larvae of Lepidoptera, Trichoptera, and Hymenoptera secrete silk, which is used in making cocoons and shelters and in food gathering by net-spinning caddisflies.

The foregut is usually differentiated into a **pharynx** (phx, immediately beyond the mouth), **esophagus** (eso, a slender tube extending posteriorly from the pharynx), **crop** (cp, an enlargement of the posterior portion of the foregut), and **proventriculus**. At its posterior end is the **stomodaeal valve**, which regulates the passage of food between the foregut and midgut. In some groups, such as cockroaches and termites, the proventriculus may bear an armature of teeth internally; these are used to further crush the food before it enters the midgut. The intima is secreted by the foregut epithelium and is relatively impermeable. The intima and epithelium are often longitudinally folded. Outside of the epithelium is an inner layer of longitudinal muscles and an outer layer of circular muscles. The longitudinal muscles sometimes have insertions on the intima. The anterior part of the foregut is provided with dilator muscles, which have their origins on the walls and apodemes of the head and thorax and their insertions on the stomodaeal muscle layers, the epithelium, or intima. These are best developed in the pharyngeal region in sucking insects, where they make the pharynx into a sucking pump. The crop is specialized for the temporary storage of food. It may be a simple enlargement of the foregut, or, as in mosquitoes and Lepidoptera, it may be a lateral diverticulum off the digestive tract. Little or no digestion of food takes place in the foregut.

The midgut (mg) is usually an elongate tube of rather uniform diameter, sometimes differentiated into two or more parts. It often bears diverticula, the **gastric caeca** (cm), near its anterior end. The midgut is not lined by cuticle. The epithelial layer of the midgut is involved both with the secretion of digestive enzymes into the lumen and in the absorption of the products of digestion into the body of the insect. Individual midgut epithelial cells are generally rather short-lived and are constantly being replaced. These dividing cells may be scattered throughout the midgut, or may be concentrated as pockets of growth. Such areas are sometimes visible from the lumen of the gut as invaginated crypts and from the outer side as bulges (called *nidi*). The midgut is the primary site of digestion and absorption in the alimentary canal. In many species, the midgut epithelium and the food are separated by a peritrophic membrane—a nonliving, permeable network of chitin and protein that is secreted by the epithelium. The function of the peritrophic membrane is unclear. It may serve to limit abrasion of the epithelium, to inhibit the movement of pathogens from the food to the insect's tissues, or as a means of separating endo- and ectoperitrophic spaces within which digestive specialization can occur.

The hindgut extends from the pyloric valve, which lies between the midgut and hindgut, to the anus. Posteriorly it is supported by muscles extending to the abdominal wall. The hindgut is generally differentiated into at least two regions, the anterior intestine and the posterior rectum (rec). The anterior intestine may be a simple tube, or it may be subdivided into an anterior ileum (il) and a posterior colon (cn). The Malpighian tubules (mt), which are excretory organs (see later), arise at the anterior end of the hindgut, and their contents empty into it. The hindgut is the final site for resorption of water, salts, and any nutrients from the feces and urine. The rectum in several species has large, thick rectal pads that are important in removing water from the feces.

The **filter chamber** is a modification of the alimentary canal in which two normally distant parts are held close together by connective tissue; it occurs in many of the Hemiptera and varies somewhat in form in different members of the order. The midgut in these insects is differentiated into three regions: the first, second, and third ventriculi. The first and second ventriculi are saclike structures immediately posterior to the esophagus, and the third ventriculus is a slender tube. Typically, the third ventriculus turns forward and comes to lie close to the first ventriculus, often coiling about it, where it is held in place by connective tissue. This complex—the first ventriculus, the coiled third ventriculus, and the connective tissue—forms the filter chamber (Figure 2–23). Beyond the filter chamber, the alimentary canal continues backward, usually as a slender tube, to enter the rectum. The Malpighian tubules emerge either from the filter chamber or just beyond it.

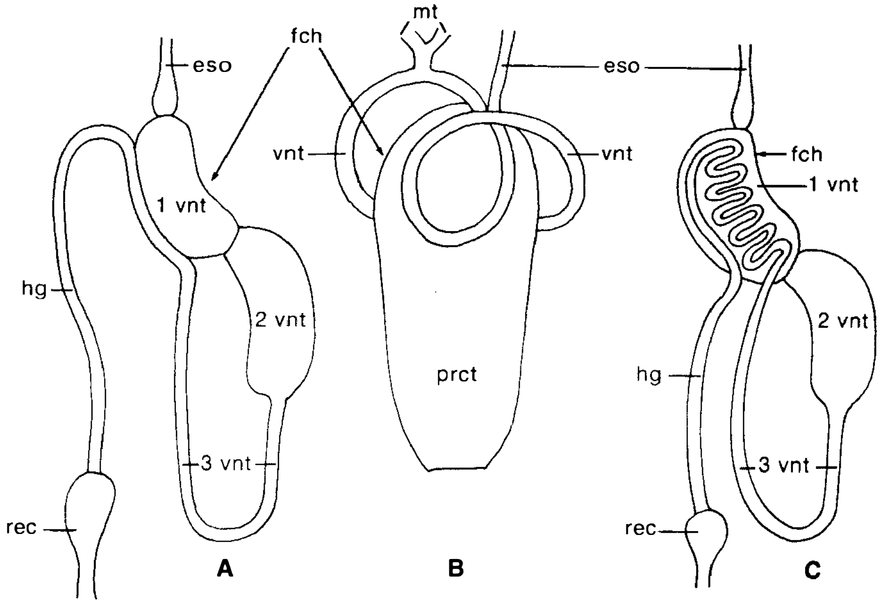

Figure 2–23 The filter chamber of Hemiptera (diagrammatic). A, A simple type of filter chamber, in which the two ends of the midgut (the first and third ventriculi) are bound together; B, The filter chamber of a scale insect (*Lecanium*); C, A filter chamber in which the posterior part of the midgut (the third ventriculus) coils about the anterior part (the first ventriculus), with the hindgut emerging from the anterior end. In A and B the junction of the midgut and hindgut (where the Malpighian tubules, which are not shown, enter the alimentary tract) is in the filter chamber. *eso*, esophagus; *fch*, filter chamber; *hg*, anterior portion of the hindgut; *mt*, Malpighian tubules; *prct*, proctodeum; *rec*, rectum; *vnt*, ventriculus (*1*, first; 2, second; *3*, third).

Many Hemiptera live on plant juices, which they usually ingest in large quantities. Entomologists think the filter chamber is a device that allows water from ingested sap to pass directly from the anterior portion of the midgut to the hindgut, concentrating sap before digestion in the posterior part of the midgut. This excess fluid passes from the anus as honeydew. However, because honeydew is often rich in nutrients such as carbohydrates and amino acids, there is some doubt about the exact function of the filter chamber.

Digestion is the process of changing food chemically and physically so that it can be absorbed and nourish various parts of the body. This process may begin even before the food is ingested but usually occurs as the ingested materials pass through the digestive tract. Solid foods are broken down by various mechanical means (chiefly the mouthparts and proventricular teeth), and all foods are subjected to a battery of enzymes as they pass through the digestive tract.

Insects feed on a great variety of living, dead, and decomposing animals, plants, and fungi and on their products. In some cases, liquids such as blood or plant juices may constitute their entire food supply. The digestive system varies considerably with the different kinds of foods consumed. The food habits may even vary greatly in a single species. Larvae and adults usually have entirely different food habits and different types of digestive systems. Some adults do not feed at all.

Most insects take food into the body through the mouth. Some larvae that live endoparasitically in a host animal can absorb food through the surface of their bodies from host tissues. Many insects have chewing mandibles and maxillae that cut, crush, or macerate food materials and force them into the pharynx. In sucking insects, the pharynx functions as a pump that brings liquid food through the beak into the esophagus. Peristaltic action moves food is along the alimentary canal.

Saliva is usually added to the food, either as it enters the alimentary canal or before, as in the case of many sucking insects that inject it into the fluids they siphon up as foods. Saliva is generally produced by the labial glands, and the labial glands of many insects also produce amylase. In certain bees, these glands secrete invertase, which is later taken into the body with nectar. In bloodsucking insects such as mosquitoes, the saliva generally contains no digestive enzymes but contains a substance that prevents coagulation of the blood and the consequent mechanical plugging of the food channel. This saliva causes the irritation produced by the bite of a bloodsucking insect.

Many insects eject digestive enzymes on food, and partial digestion may occur before the food is ingested. Flesh fly larvae discharge proteolytic enzymes onto their food, and aphids inject amylase into the plant tissues and thus digest starch in the food plant. Such extraintestinal digestion is also found in the predaceous larvae of antlions and predaceous diving beetles, and bugs that feed on dry seeds.

Most chemical digestion of the food takes place within the midgut. Some of the midgut epithelial cells produce enzymes, and others absorb digested food. Sometimes the same cells carry out secretion and absorption. Enzymes may be released into the lumen of the midgut by the disintegration of the secretory cells (holocrine secretion) or by the release of small amounts of enzymes across the cell membrane (merocrine secretion).

Only a few species of insects produce enzymes that digest cellulose, but some can use cellulose as food as a result of symbiotic microorganisms present in their digestive tracts. These microorganisms, usually bacteria or flagellated protists, can digest the cellulose, and the insects absorb the products of this digestion. Such microorganisms are present in termites and many wood-boring beetles and are often housed in special organs connected to the gut.

The fat body is a large, often somewhat amorphous organ housed in the abdomen and thorax. In many ways its function is analogous to that of the liver among vertebrates. It serves as a food reservoir and is an important site of intermediate metabolism. In some species it is also important in storage excretion (see page 27). The fat body is usually best developed in the late nymphal or larval instars. By the end of metamorphosis, it is often depleted. Some adult insects that do not feed retain their fat body in adult life.

Excretory System

The primary excretory system of an insect consists of a group of hollow tubes, the Malpighian tubules, which arise as evaginations at the anterior end of the hindgut (Figure 2–22, mt). These tubules vary in number from one to more than several hundred, and their distal, free ends are closed. These tubules function in removing nitrogenous wastes and in regulating, together with the hindgut, the balance of water and various salts in the hemolymph. Ions apparently are actively transported across the outer membrane of the tubule, generating an osmotic flow of water into the lumen. Along with this water a number of small solutes—amino acids, sugars, and nitrogenous wastes—enter the tubule passively. This primary urine is therefore an isosmotic solution containing the small molecules present in the hemolymph. Some of these solutes and the water may be actively resorbed into the hemolymph in the basal por-

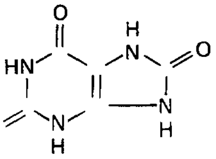

Figure 2–24 Stucture of uric acid.

tions of the Malpighian tubules or in the hindgut. The principal nitrogenous waste is usually **uric acid** (Figure 2–24), a chemical that is relatively nontoxic (and can therefore be tolerated in higher concentrations) and insoluble in water (again, recall the water balance problems inherent to a small terrestrial organism).

In some insects, most notably many beetle and moth larvae, the Malpighian tubules are bound very closely to the hindgut; these are called **cryptonephridia**. In species such as the mealworm, *Tenebrio molitor* L., that live in conditions of high drought stress, this arrangement of the tubules is apparently involved in extracting water from the fecal pellets. The mealworm, in fact, can extract water vapor from the air when the relative humidity exceeds 90%.

In addition to the Malpighian tubules, various insects have a range of methods of removing wastes or toxic substances from the hemolymph. One method is to store chemicals, such as uric acid, more or less permanently within individual cells or tissues. This process is known as storage excretion. Cockroaches store uric acid in their fat body, and the white pigment in the scales of pierid butterflies derives from uric acid stored within them. At the anterior end of the dorsal blood vessel may be a group of cells, the pericardial cells, that are important in absorbing and breaking down colloidal particles in the hemolymph. In other cases, similar cells may be widely distributed throughout the hemocoel.

Circulatory System

The principal function of the blood, or **hemolymph**, is the transport of materials—nutrients, hormones, wastes, and so forth. In most cases it plays a relatively minor role in the transport of oxygen and carbon dioxide. The hemolymph is also involved in osmoregulation, the balance of salts and water in the body; this function also involves other organs, particularly the Malpighian tubules and the rectum. The hemolymph has an important skeletal function—for example, in molting, in the expansion of the wings after the last molt, and in the protrusion of eversible structures such as eversible vesicles and genitalia. It may also function in the animal's internal defenses, in the phagocytic action of hemocytes against invading microorganisms, in plugging wounds, and in walling off certain foreign bodies such as endoparasites. Finally, the hemolymph is also a storage tissue, serving as a reservoir for water and such food materials as fat and carbohydrates.

The circulatory system of an insect is open. The main (and often only) blood vessel is located dorsal to the alimentary tract and extends through the thorax and abdomen (Figure 2–22). Elsewhere the hemolymph flows unrestricted through the body cavity (the hemocoel). The posterior part of the dorsal blood vessel, which is divided by valves into a series of chambers, is the heart (hr), and the slender anterior part is the **aorta** (ao). Extending from the lower surface of the heart to the lateral portions of the terga are pairs of sheetlike muscle bands. These constitute a dorsal diaphragm more or less separating the region around the heart (the pericardial sinus) from the main body cavity (or perivisceral sinus, sometimes further divided into a perivisceral sinus and a perineural sinus). The heart is provided with paired lateral openings called *ostia,* one pair per heart chamber, through which hemolymph enters the heart. The number of ostia varies in different insects. Some have as few as two pairs.

The hemolymph is usually a more or less clear fluid in which are suspended a number of cells (the hemocytes). It may be yellowish or greenish but is only rarely red (as in some aquatic midge larvae and some aquatic Hemiptera, owing to the exceptional presence of hemoglobin). It makes up from 5% to 40% of the body weight (usually about 25% or less).

The liquid part of the hemolymph (the plasma) contains a great many dissolved substances (such as salts, sugars, proteins, and hormones). These vary considerably—in different insects and in the same insect at different times. The plasma contains very little oxygen; the transport of oxygen is the function of the respiratory system and is decoupled from the circulatory system.

The hemocytes vary considerably in number—from about 1000 to 100,000 per mm^3—but average about 50,000 per mm^3. These cells vary greatly in shape and function. Some circulate with the hemolymph, and some adhere to the surface of tissues. The functions of the various types of hemocytes are not well known, but many are capable of phagocytosis. They may ingest bacteria, and they play a role in removing dead cells and tissues during metamorphosis. The hemolymph of different insects differs in clotting ability; the hemocytes may migrate to wounds and form a plug. Hemocytes often congregate around foreign bodies such as parasitoids and parasites, forming a sheath around them and walling them off from the body tissues. Other than the action of these hemocytes, insects have no immune system comparable to the antibodies of vertebrates (thus facilitating tranplantation experiments).

Hemolymph is moved about by pulsations of the heart and in other parts of the body, such as the base of the legs and wings, by accessory pulsatile organs. The heartbeat is a peristaltic wave that starts at the posterior end of the dorsal blood vessel and moves forward. Hemolymph enters the heart through the ostia, which are closed during the systolic phase of the heartbeat, and is pumped anteriorly. The rate of the heartbeat varies greatly: Observed rates in different insects range from 14 to about 160 beats per minute. This rate increases during periods of increased activity. The pulsations of the heart may be initiated within the heart muscle (myogenic), or they may be under nervous control (neurogenic). A reversal of the direction of the peristaltic wave of contractions, thus moving the hemolymph backward instead of forward, is not unusual.

Very little pressure develops in the general flow of hemolymph through the body. The hemolymph pressure may sometimes be less than atmospheric pressure. It can be increased by muscular contraction and compression of the body wall or by dilation of the alimentary canal (produced by swallowing air). This is how pressure is developed to break out of the remainder of the old exoskeleton at molting time and to inflate the wings.

Respiratory System

Gas transport in insects is the function of the tracheal system. The circulatory system of insects, unlike that of vertebrates, usually plays only a minor role in this process.

The tracheal system (Figure 2–25) is a system of cuticular tubes (the tracheae) that externally open at the spiracles (spr) and internally branch and extend throughout the body. They terminate in very fine closed branches, called **tracheoles**, that permeate and actually penetrate the living tissues (indenting but not actually breaking through the cell membranes). The tracheae are lined with a layer of cuticle, and in the larger branches this is thickened to form helical rings, called **taenidia**, that simultaneously give the tracheae strength (against collapse) and flexibility (to bend and twist). The tracheoles (also lined with cuticle) are minute intracellular tubes with thin walls, and they often contain fluid. It is across the walls of the tracheoles that gas exchange actually takes place.

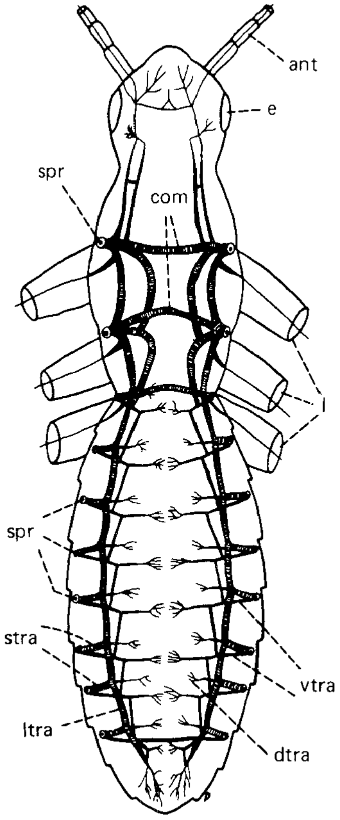

Figure 2–25 Diagram of a horizontal section of an insect showing the arrangement of the principal tracheae. *ant*, antenna; *com*, commissural trachea; *dtra*, dorsal trachea; *e*, compound eye; *l*, legs; *ltra*, main longitudinal tracheal trunk; *spr*, spiracles; *stra*, spiracular trachea; *vtra*, ventral tracheae.

The spiracles are located laterally in the pleural wall and vary in number from 1 to 10 pairs (some species have no functional spiracles). There is typically a pair on the anterior margin of both the meso- and metathorax, and a pair on each of the first eight (or fewer) abdominal segments. They vary in size and shape and usually have some sort of valvelike closing device. These valves therefore play an important role in retaining body water.

In insects with an open tracheal system (that is, with functional spiracles), air enters the body through the spiracles, then passes through the tracheae to the tracheoles, and oxygen ultimately enters body cells by diffusion. Carbon dioxide leaves the body in similar fashion. The spiracles may be partly or completely closed for extended periods in some insects. Water loss through the spiracles may be minimized in this way.

Insects generally have longitudinal tracheal trunks (connectives, ltra) connecting the tracheae from adjacent spiracles on the same side of the body and transverse commissures (com) connecting the tracheae on opposite sides of the body, so that the entire system is interconnected. The movement of air through the tracheal system is by simple diffusion in many small insects, but in most larger insects this movement is augmented by active ventilation, chiefly by the abdominal muscles; the movements of the internal organs, or of the legs and wings, may also aid ventilation. Where ventilation occurs, air may move in and out of each spiracle, but generally enters through the anterior spiracles and leaves by the posterior ones. This flow of air through the tracheal system is effected by controlling which spiracles are open and when. Sections of the main tracheal trunks are often dilated to form air sacs, which help in ventilation.

Closed tracheal systems have the spiracles permanently closed but have a network of tracheae just under the integument, distributed either widely over the body or particularly below certain surfaces (the gills). Some aquatic and parasitic insects have closed systems. In these species, gases enter and leave the body by diffusion across the body wall between the tracheae and the external environment, and gases move through the tracheal system by diffusion.

A great many insects live in water; these get their oxygen from one (rarely both) of two sources: the oxygen dissolved in the water or atmospheric oxygen. Gas exchange in many small, soft-bodied aquatic nymphs and larvae (and possibly some adults) occurs by diffusion through the body wall, usually into and out of a tracheal system. The body wall in some cases is unmodified except perhaps for having a fairly rich tracheal network just under the integument. In other cases, there are special thin extensions of the body wall that have a rich tracheal supply and through which gas exchange occurs. These structures, called *tracheal gills*, come in a variety of shapes and may be located on different parts of the body. The gills in mayfly nymphs are in the form of leaflike structures on the sides of the first seven abdominal segments (Figure 9-2). In dragonfly nymphs, they are folds in the rectum, and water is moved into and out of the rectum and over these folds. In damselfly nymphs, the gills are three leaflike structures at the end of the abdomen as well as folds in the rectum (Figure 10-1). In stonefly nymphs, the gills are fingerlike or branched structures located around the bases of the legs or on the basal abdominal segments (Figure 16-2B). Gas exchange may occur through the general body surface of these insects, and in some cases (such as damselfly nymphs), the exchange through the body surface may be more important than that through the tracheal gills.

Insects that live in water and get their oxygen from atmospheric air do this in one of three general ways: from air spaces in submerged parts of certain aquatic plants, through spiracles placed at the water surface (with the body of the insect submerged), or from a film of air held somewhere on the surface of the body while the insect is submerged. A few larvae (for example, those of the beetle genus *Donacia* and the mosquito genus *Mansonia*) have their spiracles in spines at the posterior end of the body, and these spines are inserted into the air spaces of submerged aquatic plants. Many aquatic insects (for example, waterscorpions, rattailed maggots, and the larvae of culicine mosquitoes) have a breathing tube at the posterior end of the body, which is extended to the surface. Hydrophobic hairs around the end of this tube enable the insect to hang from the surface film, and they prevent water from entering the breathing tube. Other aquatic insects (for example, backswimmers and the larvae of anopheline mosquitoes) get air through posterior spiracles placed at the water surface. These insects do not have an extended breathing tube.

The insects that get their oxygen from atmospheric air at the water surface do not spend all their time at the surface. They can submerge and remain underwater for a considerable period, getting oxygen from an air store either inside or outside the body. The air stores in the tracheae of a mosquito larva, for example, enable the larva to remain underwater for a long time.

Many aquatic bugs and beetles carry a thin film of air somewhere on the body surface when they submerge. This film is usually under the wings or on the ventral side of the body. The air film acts like a physical gill, with dissolved oxygen in the water diffusing into the bubble when the partial pressure of oxygen in the film falls below that of the water. The insect may get several times as much oxygen from this temporary structure as was originally in it, because of gas exchanges between the air film and the surrounding water. A few insects (for example, elmid beetles) have a permanent layer of air around the body surface, held there by a body covering of thick, fine, hydrophobic hairs; such a layer is called a **plastron**. The air reservoirs of aquatic insects not only play a role in gas exchange but also may have a hydrostatic function (like the swim bladder of fish). Two crescent-shaped air sacs in *Chaoborus* larvae (Diptera: Chaoboridae, Figure 34-30A) are apparently used to regulate this insect's specific gravity: to hold it perfectly motionless or to enable it to migrate up or down in the water column.

Parasitic insects that live inside the body of their host get oxygen from the body fluids of the host by diffusion through their integument, or (for example, in tachinid fly larvae) their posterior spiracles may be extended to the body surface of the host or attach to one of the host's tracheal trunks.

Body Temperature

Insects are generally considered cold-blooded or poikilothermic; that is, their body temperature rises and falls with the environmental temperature. This is the case with most insects, particularly if they are not very active, but the action of the thoracic muscles in flight usually raises the insect's temperature above that of the environment. The cooling of a small object is fairly rapid, and the body temperature of a small insect in flight is very close to that of the environment. In insects such as butterflies and grasshoppers, the body temperature in flight may be 5°C or 10°C above the environmental temperature, and in insects such as moths and bumble bees (which are insulated with scales or hair), the metabolism during flight may raise the temperature of the flight muscles 20°C or 30°C above the environmental temperature.

With most flying insects, the temperature of the flight muscles must be maintained above a certain point to produce the power necessary for flight. Many larger insects may actively increase the temperature of their flight muscles before flight by a "shivering" or a vibration of the wing muscles.

Honey bees remain in the hive during the winter, but do not go into a state of dormancy at the onset of cold weather (as most other insects do). When the temperature gets down to about 14°C, they form a cluster in the hive and, by the activity of their thoracic muscles, maintain the temperature of the cluster well over 14°C (as high as 34°C to 36°C when they are rearing brood).

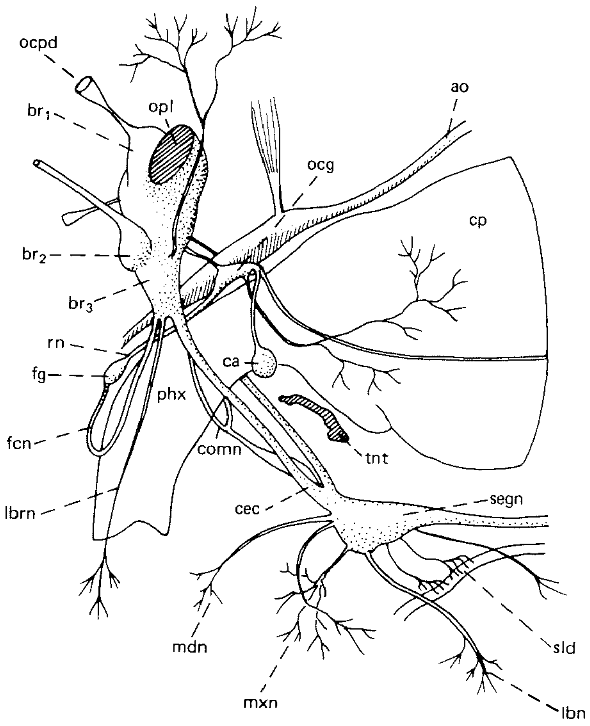

Figure 2–26 Anterior part of the nervous system of a grasshopper. *ao*, dorsal aorta; br_1, protocerebrum; br_2, deutocerebrum; br_3, tritocerebrum; *ca*, corpus allatum; *cec*, circumesophageal connective; *comn*, tritocerebral commissure; *cp*, crop; *fcn*, frontal ganglion connective; *fg*, frontal ganglion; *lbn*, labial nerve; *lbrn*, labral nerve; *mdn*, mandibular nerve; *mxn*, maxillary nerve; *ocg*, occipital ganglion; *ocpd*, ocellar pedicel; *opl*, optic lobe; *phx*, pharynx; *rn*, recurrent nerve; *segn*, subesophageal ganglion; *sld*, salivary duct; *tnt*, tentorium. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

Nervous System

The central nervous system of an insect consists of a brain in the head above the esophagus, a **subesophageal** ganglion (Figure 2–26, segn) connected to the brain by two nerves (the circumesophageal connectives, cec) that extend around each side of the esophagus, and a ventral nerve cord extending posteriorly from the subesophageal ganglion. The brain consists of three pairs of lobes, the **protocerebrum** (br$_1$), **deutocerebrum** (br$_2$), and **tritocerebrum** (br$_3$). The protocerebrum innervates the compound eyes and ocelli, the deutocerebrum innervates the antennae, and the tritocerebrum innervates the labrum and foregut. The two lobes of the tritocerebrum are separated by the esophagus and are connected by a commissure that passes under the esophagus (comn). The ventral nerve cord (Figure 2–22, nc) is typically double and has segmental ganglia (Figure 2–22, gn). Frequently some of these ganglia are fused, particularly toward the end of the abdomen, resulting in fewer visible ganglia than segments.

The ganglia of the central nervous system (brain, subesophageal ganglion, and segmental ganglia of the central nerve cord) serve as the coordinating centers. Each of these has a certain amount of autonomy; that is, each may coordinate the impulses involved in activities in particular regions of the body. Activities involving the entire body may be coordinated by impulses from the brain, but many of these can occur with the brain absent.

Sense Organs

An insect receives information about its environment (including its own internal environment) through its sense organs. These organs are located mainly in the body wall, and most are microscopic in size. Each is usually excited only by a specific stimulus. Insects have sense organs receptive to chemical, mechanical, auditory, and visual stimuli, and possibly such stimuli as relative humidity and temperature.

Chemical Senses

Chemoreceptors—those involved in the senses of taste (gustation) and smell (olfaction)—are important parts of an insect's sensory system and are involved in many types of behavior. Feeding, mating, habitat selection, and parasite–host relationships, for example, are often directed by the insect's chemical senses.

Generally each sensillum consists of a group of sensory cells whose distal processes form a bundle extending to the body surface (Figure 2–27C). The endings of the sensory processes are usually in a thin-walled, peglike structure (scn). The peglike process may be sunk in a pit, or the sensory processes may end in a thin cuticular plate set over a cavity in the cuticle. In some cases the endings of the sensory processes may lie in a pit in the body wall and may not be covered by cuticle.

The organs of taste are located principally on the mouthparts, but some insects (for example, ants, bees, and wasps) also have taste organs on the antennae, and many (for example, butterflies, moths, and flies) have taste organs on the tarsi.

The exact mechanism by which a particular substance initiates a nerve impulse in the sensory cells of a chemoreceptor is not completely understood. The substance may penetrate to the sensory cells and stimulate them directly, or it may react with something in the receptor to produce one or more other substances that stimulate the sensory cells. In any event, an insect's sensitivity to different substances varies; two very similar chemicals (such as the dextro and levo forms of a particular sugar) may be quite different in their stimulating effect. Some scents (for example, the sex attractant produced by a female) can be detected by one sex (in this case, the male) but not by the other. The sensitivity of chemoreceptors to some substances is very high. Many insects can detect certain odors at very low concentrations up to a few miles from their source.

Mechanical Senses

Insect sense organs sensitive to mechanical stimuli react to touch, pressure, or vibration, and provide the insect with information that may guide orientation, general movements, feeding, flight from enemies, reproduction, and other activities. These sense organs are of three principal types: hair sensilla, campaniform sensilla, and scolopophorous organs.

The simplest type of tactile receptor is a hair sensillum (Figures 2–27A and 2–28). A process from the sensory neuron extends to the base of the seta, and movements of the seta initiate impulses in the neuron.

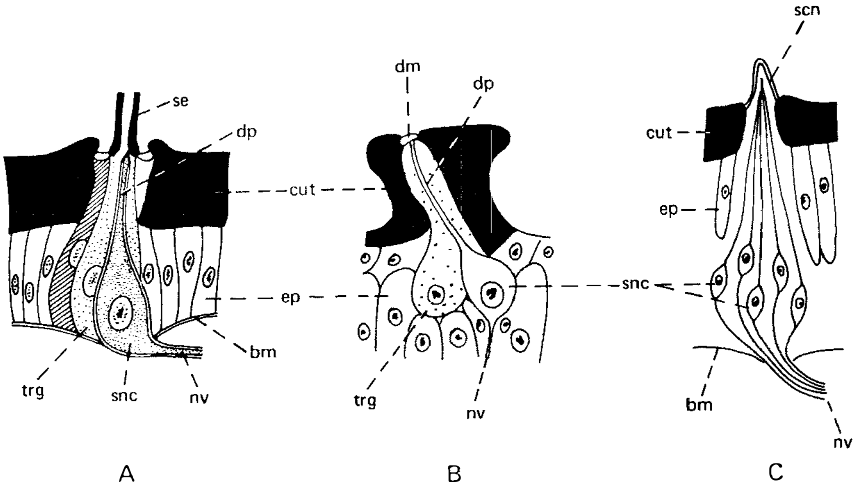

Figure 2–27 Insect sensilla. A, Hair sensillum; B, Campaniform sensillum; C, Chemoreceptor. *bm*, basement membrane; *cut*, cuticle; *dm*, domelike layer of cuticle over nerve ending; *dp*, distal process of sensory cell; *ep*, epidermis; *nv*, neuron; *scn*, sense cone; *se*, seta; *snc*, sensory cell; *trg*, trichogen cell. (A, C, Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

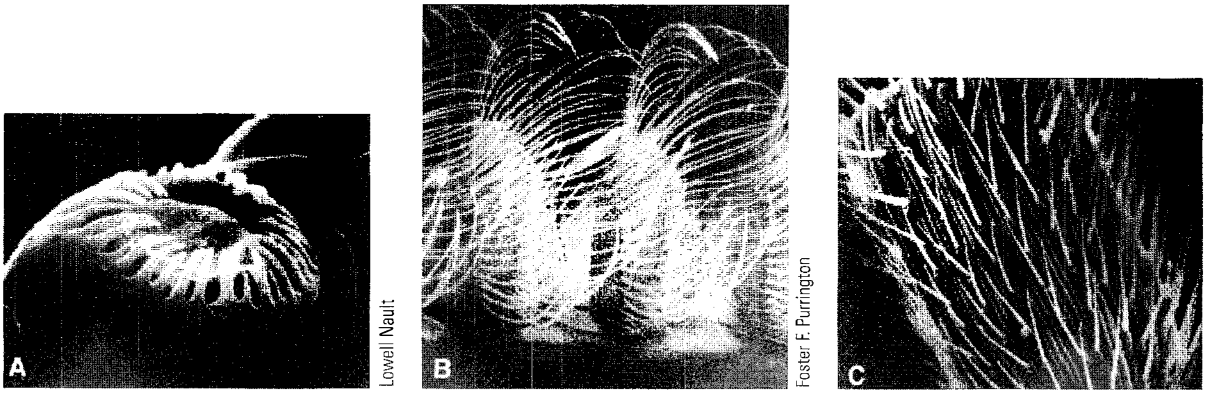

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Figure 2–28 Scanning electron microscope photographs of some insect sensilla. A, Sensilla on the antenna of an aphid, 1750×; B, Hair sensilla on the antenna of a clearwing moth, 95×; C, Hair sensilla on the antenna of a braconid, 500×.

In a campaniform sensillum, the neuron ending lies just under a domelike area of the cuticle (Figure 2–27B), and distortion of this dome elicits a neuronal response. Scolopophorous organs (also known as *chordotonal organs*) are more complex sensilla that consist of a bundle of sensory neurons whose dendrites are attached to the body wall; they are sensitive to movements of the body (including pressure and vibration). These organs, which are widely distributed over the body, include the subgenual organs (usually located within the proximal end of the tibiae), Johnston's organ (in the second antennal segment, sensitive to movements of the antennal flagellum), and the tympanal organs (involved in hearing). Mechanical stimuli act by displacement. The stimuli may come from outside the insect (for example, touch and hearing) or from inside it (stimuli resulting from position or movement). The mechanical stimuli initiate a series of nerve impulses, the character of which is determined by the stimulus. In some cases, the nerve impulses may be transmitted at frequencies as high as several hundred per second.

The sense of touch in insects operates mainly through hair sensilla (trichoid sensilla). The character of the nerve impulses initiated is determined by the rate and direction of the hair deflection. This sense is generally quite acute: Very little hair deflection may be necessary to initiate a series of neuronal impulses.

Many insects show a response to gravity, for example, in the surfacing of aquatic insects and in the vertical constructions (burrows in the ground, combs in a beehive, and the like) some insects make. Insects generally do not have organs of equilibrium comparable to the statocysts of crustaceans, although air bubbles carried on the body surfaces by certain aquatic insects when they submerge may act in a similar manner. The forces of gravity and pressure generally are detected by other means.

Many joints in insects have tactile setae that register any movements, providing the insect with information on the position of the joint (this is known as *proprioception*). Pressure on the body wall, whether produced by gravity or some other force, is usually detected by campaniform sensilla. Pressure on the legs may be detected by subgenual organs or by sensitive setae on the tarsi.

An insect detects movements of the surrounding medium (air or water currents) chiefly by tactile setae. It receives information on its own movements both by mechanoreceptors and by visual cues. Movements of air or water past an insect (whether the insect is stationary and the medium is moving, or the insect is moving) are detected largely by the antennae or sensory setae on the body. In the Diptera and Hymenoptera, the antennae seem the most important detectors of such movements. In other insects, sensory setae on the head or neck may be the most important receptors. The halteres of the Diptera play an important role in maintaining equilibrium in flight. They move through an arc of nearly 180 degrees at rates of up to several hundred times per second. Any change in the insect's direction strains the cuticle because of the gyroscopic property of the rapidly beating halteres and is detected by the campaniform sensilla distributed on the base of the haltere.

Hearing

The ability to detect sound (vibrations in the substrate or in the surrounding medium) is developed in many insects, and sound plays a role in many types of behavior. Insects detect airborne sounds by means of two types of sense organs, hair sensilla and tympanal organs. They detect vibrations in the substrate subgenual organs.

Many insects apparently can detect sound, but entomologists do not always know which sensilla are involved. In some of the Diptera (for example, mosquitoes), however, entomologists know that the setae of the antennae are involved in hearing (the sensilla being Johnston's organ in the second antennal segment).

Tympanal organs are scolopophorous organs in which the sensory cells are attached to (or very near to) tympanic membranes. The number of sensory cells involved ranges from one or two (for example, in certain moths) up to several hundred. The tympanic membrane (or tympanum) is a very thin membrane with air on both sides of it. Tympanal organs are present in certain Orthoptera, Hemiptera, and Lepidoptera. The tympana of short-horned grasshoppers (Acrididae) are located on the sides of the first abdominal segment. Those of katydids (Tettigoniidae) and crickets (Gryllidae), when present, are located at the proximal end of the front tibiae (Figure 2–8D, tym). The tympana of cicadas are located on the first abdominal segment (Figure 22-45, tym). Moths may have tympana on the metathorax or the base of the abdomen.

Vibrations in the substrate may be initiated in the substrate directly or may be induced (through resonance) by airborne sound vibration. The detection of substrate vibration is mainly by subgenual organs. The frequency range to which these organs are sensitive varies in different insects, but is mainly between about 200 and 3000 Hz. Some insects (for example, bees) may be largely insensitive to airborne sound but can detect sound vibrations reaching them through the substrate.

The sensory setae that detect airborne sound are generally sensitive only to relatively low frequencies (a few hundred Hertz or less; rarely, a few thousand). Probably the most efficient auditory organs in insects are the tympanal organs. These are often sensitive to frequencies extending well into the ultrasonic range (up to 100,000 Hz or more),[2] but their discriminatory ability is targeted to amplitude modulation rather than to frequency modulation. An insect's response (its behavior and the nerve impulses initiated in the auditory nerves) is not affected by differences in the frequencies of the sound as long as these frequencies are within the detectable range; an insect thus does not detect differences (or changes) in the pitch of a sound, at least at the higher frequencies. In contrast, tympanal organs are very sensitive to amplitude modulation, that is, the rhythmic features of the sound. These are the most important features of an insect's "song."

Vision

The primary visual organs of insects generally are of two types, the frontal ocelli (singular, *ocellus*) and the many-faceted compound eyes.

Ocelli have a single corneal lens that is somewhat elevated or domelike; beneath this lens are two cell layers, the corneagenous cells and the retina (Figure 2–29A). The corneagenous cells, which secrete the cornea, are transparent. The light-sensitive portion of insect photoreceptors consists of closely packed microvilli on one side of the retinal cells called the *rhabdom*. In the ocelli, the rhabdoms are in the outer part of the retina. The basal portions of the retinal cells are often pigmented. The ocelli apparently do not form focused images (the light is focused below the retina); they seem to be organs sensitive mainly to differences in light intensity.

The most complex light receptors in insects are the compound or faceted eyes, which consist of many (up to several thousand) individual units called ommatidia (Figure 2–29C,D). Each ommatidium is an elongate group of cells capped externally by a hexagonal corneal lens. The corneal lenses are usually convex externally, forming the facets of the eye. Beneath this corneal lens is usually a crystalline cone of four Semper cells (Figure 2–29D, cc) surrounded by two pigmented corneagenous cells (pgc), and beneath the crystalline cone is a group of elongate sensory cells, usually eight in number, surrounded by a sheath of epidermal pigment cells (pgc). The striated portions of the sensory cells form a central or axial rhabdom (rh) in the ommatidium.

The pigment surrounding an ommatidium (Figure 2–29D, pgc) generally extends far enough inward so that the light reaching a rhabdom comes through just the one ommatidium; the image the insects gets is thus a mosaic, and such an eye is spoken of as an *apposition eye*. If the pigment is located more distally in relation to the rhabdom, light from adjacent ommatidia may reach a given rhabdom; this is a superposition eye. In some insects that fly both day and night, such as moths, the migration of the pigment around an ommatidium operates somewhat like the iris of the human eye: In bright light, the pigment migrates inward, surrounding the rhabdom so that the only light reaching the rhabdom is that coming through that ommatidium (an apposition eye); in the dark, the pigment moves outward, so that light from adjacent ommatidia can also reach the rhabdom (a superposition eye). The time

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[2] The upper limit of hearing in humans is generally about 15,000 Hz.

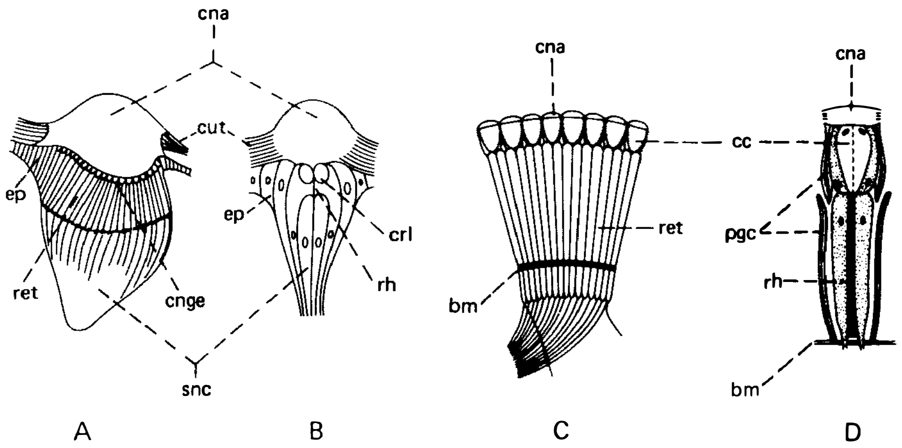


Figure 2–29 Eye structure in insects (diagrammatic). A, Dorsal ocellus of an ant; B, Lateral stemma of a caterpillar; C, Vertical section of part of a compound eye; D, Ommatidium of a compound eye. *bm*, basement membrane; *cc*, crystalline cone; *cna*, cornea; *cnge*, corneagenous cells; *crl*, crystalline lens; *cut*, cuticle; *ep*, epidermis; *pgc*, pigment cells; *ret*, retina; *rh*, rhabdom; *snc*, sensory cells of retina. (B, C, Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press; D, Redrawn from Matheson 1951, *Entomology for Introductory Courses*, 1947.)

required for this movement of the pigment varies in different species. For the codling moth, it is from 30 to 60 minutes.

Many immature insects (and some adults) lack compound eyes, and in their place may be small groups of visual organs similar to ocelli in external appearance (Figure 2–29B). These are called *stemmata* (or sometimes *lateral ocelli*). These structures are quite varied in their structure, but all appparently represent highly modified compound eyes (see Paulus 1979). In most larvae of Holometabola, the larval eyes degenerate during metamorphosis and are replaced by new adult compound eyes.

The flicker-fusion frequency in insects (the rate of flicker at which the light appears continuous) is much higher than in humans: 45 to 53 per second in humans and up to 250 or more in insects. This higher rate means that insects can perceive form even when in rapid flight and that they are very sensitive to motion. In some insects (for example, dragonflies), the ommatidia of one eye are oriented so that their axes intersect with those of the other eye, allowing steroscopic vision. If a dragonfly nymph is blinded in one eye, the nymph cannot judge the position of its prey very accurately.

The range in wavelength to which insect eyes are sensitive is from about 2540 to 6000 Å, compared with about 4500 to 7000 Å in humans. Insects' visual range is shifted to shorter wavelengths in comparison to that of vertebrates. Many insects appear to be color blind, but some can distinguish colors, including ultraviolet. The honey bee, for example, can distinguish blue and yellow but cannot see red. Just how an insect distinguishes different colors is not clear. There is evidence it may result from different retinal cells being sensitive to light of different wavelengths. Some insects (for example, the honey bee) are able to analyze polarized light. From the pattern of polarization in a small patch of sky, they can determine the position of the sun. The head capsule of some weevils contains a region that transmits only far-red and near-infrared light. In the alfalfa weevil, *Hypera postica*, this extraocular cutoff filter apparently works in conjunction with the compound eyes, enabling the insect to use visual cues in locating and recognizing its host plant.

Other Sense Organs

Insects usually have a well-developed temperature sense. The sense organs involved are distributed over the body but are more numerous on the antennae and legs. Some insects also have a well-developed humidity sense. The sensilla involved in these senses are quite diverse in structure, and in many cases the relationship between the observed structure and function is not well understood (see Altner and Loftus 1985).

Endocrine System

Several organs in an insect are known to produce hormones, the principal functions of which are the control of the reproductive processes, molting, and metamorphosis. Chemicals similar to hormones of vertebrates, including androgens, estrogens, and insulin, have been detected in insects, but their function is yet unknown.

The neurosecretory cells in the brain are neurons that produce one or more hormones that play a role in growth, metamorphosis, and reproductive activities. One of these, commonly called the *brain hormone* or *prothoracicotropic hormone (PTTH)*, plays an important role in molting by stimulating a pair of glands in the prothorax to produce the hormone ecdysone that causes apolysis. Other hormones produced by the brain may have other functions. For example, entomologists believe that a brain hormone plays a role in caste determination in termites and in breaking diapause in some insects.

Ecdysone (Figure 2–30A) initiates growth and development and causes apolysis. This hormone occurs in all insects groups that have been studied, in crustaceans, and in arachnids, and it is probably the molting hormone of all arthropods. It also plays a role in the differentiation of the ovarioles and accessory reproductive glands in females and in several steps in the process of egg production (oogenesis). Ecdysone, in fact, is also produced within the ovaries of insects.

The corpora allata (Figure 2–26, ca) produce a hormone called the *juvenile hormone* (JH) (Figure 2–30B), the effect of which is the inhibition of metamorphosis. Various substances, particularly terpenes such as farnesol, show considerable juvenile hormonelike activity. JH also has effects on other processes besides the inhibition of metamorphosis. It is involved in vitellogenesis, accessory reproductive gland activity, pheromone production, and sexual behavior (see Raabe 1986).

Substances chemically related to ecdysone and juvenile hormone occur in certain plants and may protect the plants from feeding by insects. Chemical analogs of ecdysone and juvenile hormone are being studied to see whether they can function as new kinds of insecticides.

Reproductive Systems

Internal Reproductive Systems

The internal reproductive system of the female (Figure 2–31A) consists of a pair of ovaries (ovy), a system of ducts through which the eggs pass to the outside, and associated glands. Each ovary generally consists of a group of ovarioles (ovl). These lead into the lateral oviduct posteriorly (ovd) and unite anteriorly in a suspensory ligament (sl) that usually attaches to the body wall or to the dorsal diaphragm. The number of ovarioles per ovary varies from 1 to 200 or more, but it is usually in the range of 4 to 8. Oogonia (the primary germ cells) are located in the anterior apical portion of the ovariole, the germarium. The oogonia undergo mitosis, giving rise to the oocytes and trophocytes (or nurse cells; entomologists do not know what mechanism determines which daughter cells become oocytes and which become trophocytes). Ovarioles in which trophocytes are produced are called *meroistic ovarioles*; no trophocytes are produced in panoistic ovarioles. The oocytes pass down through the ovarioles, maturing as they go. Thus the spatial sequence in the ovariole reflects the temporal sequence of oocyte matura-

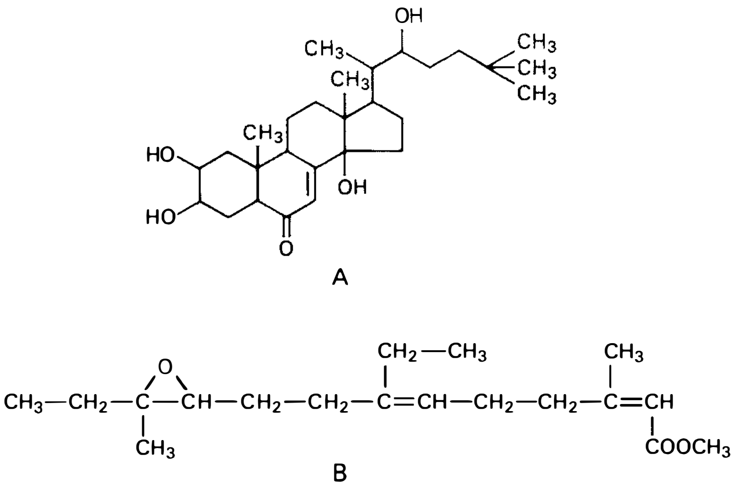


Figure 2–30 Structure of two insect hormones. A, Ecdysone; B, Juvenile hormone.

tion. The trophocytes may be connected to the oocyte by cytoplasmic filaments and may remain in the germarium (telotrophic ovarioles) or pass down the ovariole with each oocyte (in polytrophic ovarioles). The trophocytes are important in passing ribosomes and RNA to the oocyte. An oocyte, the surrounding epithelium, and trophocytes (in polytrophic ovarioles) together form a follicle. Yolk proteins (vitellogenins) are synthesized outside the ovariole and transported into the oocyte by the follicular epithelium. In this region of the ovariole (the vitellarium), the oocytes greatly increase in size owing to the deposition of yolk (the process of vitellogenesis). Yolk consists of protein bodies (largely derived from hemolymph proteins), lipid droplets, and glycogen. Many insects harbor microorganisms in their bodies, and in some cases these may get into the egg during its development, usually through the follicle cells. The maturation divisions of the oocyte may occur at about the end of vitellogenesis or even after insemination, resulting in eggs with the haploid number of chromosomes. In the lower portion of the ovariole, a vitelline membrane forms around the oocyte, and the follicular epithelium secretes the chorion (or eggshell) around the mature oocyte.

In many insects, all or most of the oocytes mature before any are laid, and the egg-swollen ovaries may occupy a large part of the body cavity and may even distend the abdomen. The two lateral oviducts usually unite posteriorly to form a single common (or median) oviduct, which enlarges posteriorly into a genital chamber or vagina. The vagina extends to the outside, the opening being called either the *ovipore* (in reference to the opening through which the eggs are laid) or *vulva* (the copulatory opening). Because the vagina usually also receives the male genitalia during copulation, it is sometimes known as the *bursa copulatrix*. Associated with the vagina are usually a saclike structure called the *spermatheca*, in which spermatozoa are stored, and often various accessory glands, which may secrete adhesive material to fasten the eggs to some ob-

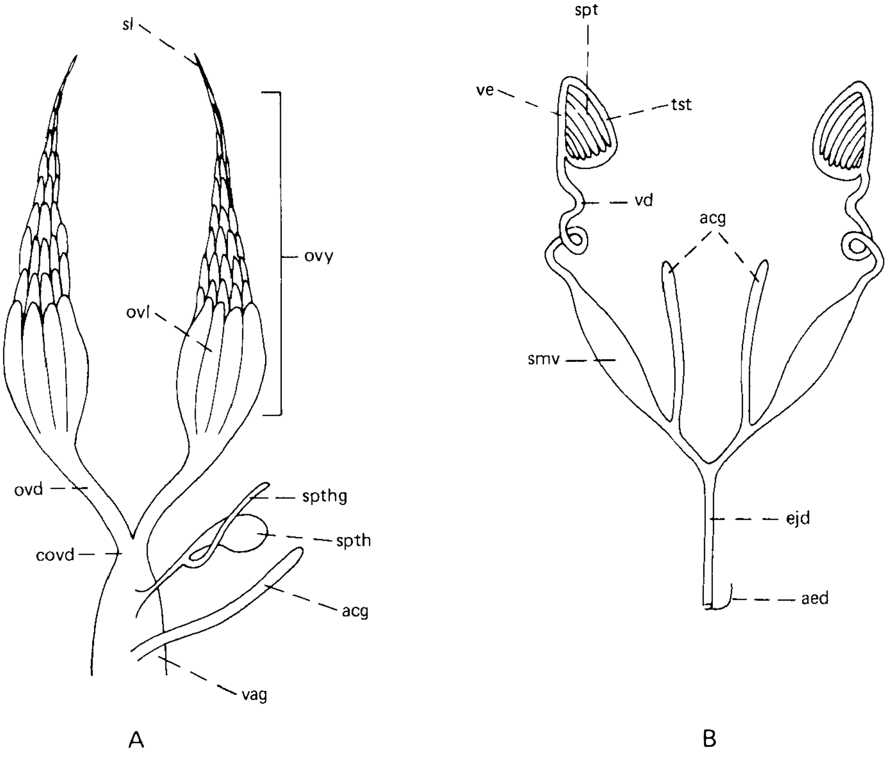


Figure 2–31 Reproductive systems of insects. A, Female reproductive system; B, Male reproductive system. *acg*, accessory gland; *aed*, aedeagus; *covd*, common oviduct; *ejd*, ejaculatory duct; *ovd*, oviduct; *ovl*, ovariole; *ovy*, ovary; *sl*, suspensory ligament; *smv*, seminal vesicle; *spt*, sperm tube; *spth*, spermatheca; *spthg*, spermathecal gland; *tst*, testis; *vag*, genital chamber or vagina; *vd*, vas deferens; *ve*, vas efferens. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

ject or provide material that covers the egg mass with a protective coating.

In many Lepidoptera (the Ditrysia), there are two openings to the reproductive tract of the female. The common oviduct leads to the vagina and the ovipore to the outside on segment 9. During copulation, however, the male places his genitalia and deposits the spermatophore in a separate opening, the vulva, on segment 8. The vulva leads to the bursa copulatrix, which is connected to the vagina and thence to the spermatheca by a sperm duct, through which the spermatozoa must move.

Egg development is usually complete about the time the adult stage is reached, but in some cases it is completed later. In those aphids in which the female gives birth to living young parthenogenetically, the eggs are matured and development begins before the adult stage is reached. In the beetle genus *Micromalthus*, the eggs are matured and begin their development (without fertilization) in the ovaries of the larvae, and are passed to the outside (as either eggs or larvae) before the mother becomes an adult. In the cecidomyiid genus *Miastor*, egg development is also completed in the larval stage, but in this case the young larvae (which have developed parthenogenetically) break out of the ovaries into the body cavity and develop there. They eventually rupture the cuticle of the mother larva and escape to the outside. Reproduction by a preadult stage is called *paedogenesis*.

Egg production appears to be controlled in many insects by one or more hormones from the corpora allata, including juvenile hormone (Figure 2–30B), that act by controlling the initial stages of oogenesis and yolk deposition. Removal of the corpora allata prevents normal egg formation, and their reimplantation (from either a male or a female) induces ovarian activity again. The corpora allata have nerve connections with the brain, and nerve impulses affect their activity. Researchers also believe that (at least in some cases) neurosecretory cells in the brain may produce a hormone that affects the activity of the corpora allata. Many external factors (for example, photoperiod and temperature) affect egg production, and these factors probably act through the corpora allata.

The reproductive system of the male (Figure 2–31B) is similar in general arrangement to that of the female. It consists of a pair of gonads, the testes, ducts to the outside, and accessory glands. Each testis (tst) consists of a group of sperm tubes (spt) or follicles surrounded by a peritoneal sheath. Each sperm follicle opens into a short connecting tube, the vas efferens (ve; plural, vasa efferentia), and these connect to a single vas deferens (vd; plural, vasa deferentia) on each side of the animal. The two vasa deferentia usually unite posteriorly to form a median ejaculatory duct (ejd), which opens to the outside on a penis or an aedeagus (aed). Some insects have an enlargement of or a lateral diverticulum from each vas deferens in which spermatozoa are stored. These are called *seminal vesicles* (smv). The accessory glands (acg) secrete fluids that serve as a carrier for the spermatozoa or that harden about them to form a sperm-containing capsule, the spermatophore.

The sperm begin their development in the distal (anterior) ends of the sperm follicles of the testes and continue development as they pass toward the vas efferens. The processes of spermatogenesis (production of haploid germ cells from diploid spermatogonia) is usually completed by the time the insect reaches the adult stage or very shortly thereafter.

The spermatozoa of insects come in an almost bewildering variety of shapes and sizes, often differing quite strikingly from the typical tadpole-shaped cells one thinks of (see Jamieson 1987). One notable characteristic is that the flagellum, or axoneme, is made up of the typical 9 + 2 arrangement of microtubules characteristic of flagella and cilia, but in addition has an outer ring of 9 single microtubules that are derived from the ring of 9 doublets. This 9 + 9 + 2 arrangement is characteristic of hexapods as a whole. In addition to the more familiar threadlike or tadpolelike cells, some hexapods have spermatozoa with two flagella instead of one, cells in which the axoneme is "encysted" so that they are immobile, and, in some Protura, even simple disk-shaped immobile cells. Among species of *Drosophila*, the spermatozoa range in length from about 55 μm to 15 mm (the total body length of the familiar *D. melanogaster* is less than 5 mm)!

External Genitalia

The external genitalia of most insects are generally thought to be derived from appendages of abdominal segments 8, 9, and possibly 10. The male genitalia are primarily organs involved with copulation and the transfer of sperm to the female. The female genitalia are involved in depositing the eggs on or in a suitable substrate. These structures are called *external genitalia* even though they may be retracted within the apical abdominal segments when not in use and are often (especially in the male) not visible without dissection.

The appendicular ovipositor of pterygote insects is believed to have evolved from a structure similar to that now found in the female genitalia in the Thysanura (Figure 2–32A). This consists of an ovipositor, which is formed from the appendages (gonopods) of segments 8 and 9. The first gonocoxa (the first valvifer, from segment 8, gcx_1) articulates dorsally with tergum 8; the second gonocoxa (second valvifer, from segment 9, gcx_2) articulates with tergum 9. Laterally, the gono-

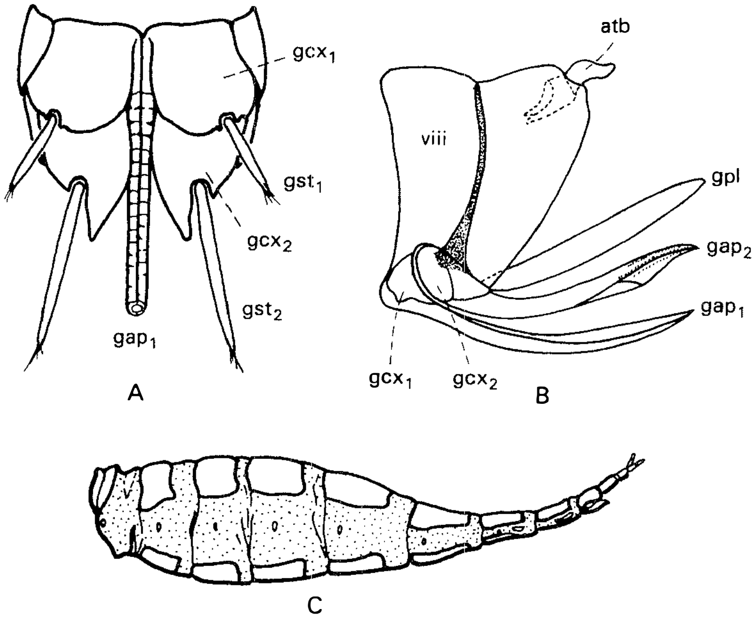


Figure 2–32 Ovipositor of insects. A, Ovipositor of Thysanura, ventral view; **B**, Ovipositor of a leafhopper, lateral view with parts spread out; C, Secondary ovipositor of Mecoptera, lateral view. *atb*, anal tube; *gcx₁*, first gonocoxa; *gcx₂*, second gonocoxa; *gap₁*, first gonapophysis; *gap₂*, second gonapophysis; *gpl*, gonoplac; *gst₁*, first gonostylus; *gst₂*, second gonostylus. (A, C, Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

coxae bear styli, the **gonostyli**; these are presumably serial homologs of the styli on the pregenital segments and thus represent the derived telopods of the primitive abdominal appendages. Medially each gonocoxa bears an elongate process known as a **gonapophysis** (also called a *valvula*); the second gonapophyses (gap_2, segment 9) lie above the first gonapophyses (gap_1, segment 8), and together these form the shaft of the ovipositor (ovp). Coordination of the movement of these four elongate structures is achieved by two mechanisms. First, the two gonapophyses on each side are connected by a tongue-in-groove mechanism known as an **olistheter**. In addition, a small sclerite on each side, the **gonangulum**, articulates with the second gonocoxa (from which it is derived), the first gonapophysis, and tergum 9. Again, this interconnects the movements of the first and second gonapophyses on each side.

In the pterygote insects that retain an appendicular ovipositor, the first gonostylus is lost, and the second gonocoxa is elongate (perhaps incorporating remnants of the second gonostylus) to form a sheathlike outer covering for the ovipositor shaft, the gonoplacs (also known as the *third valvulae*, Figure 2–32B, gpl). In most insects, the gonoplacs serve both a protective and a sensory function and are not involved in penetrating the substrate in order to oviposit. In the Orthoptera, however, the gonoplacs are cutting or digging structures, taking over the function of the second gonapophyses, which are smaller and function as egg guides.

There are a number of modifications of this basic appendicular ovipositor structure within the pterygotes, but the most generalized condition is found in some Odonata, Hemiptera (Auchenorrhyncha), Orthoptera, and Hymenoptera. In many Holometabola, the appendicular components of the ovipositor are very much smaller and are not involved in oviposition. Instead, the terminal abdominal segments form a telescoping tube, called the *pseudovipositor* or *oviscapt*, which the female extends when ovipositing (Figure 2–32C). In some cases, such as tephritid flies, this type of ovipositor bears apical cutting plates, enabling the female to place her eggs deep within a suitable substrate.

The external genitalia of male insects show such incredible diversity that it has been difficult for entomologists to infer the primitive structures from which they evolved and to homologize the parts in different orders. The genitalia of the Thysanura and Microcoryphia are generally similar to that of the females, but with an additional median penis derived from segment 10 (Figure 2–33A). However, the male geni-

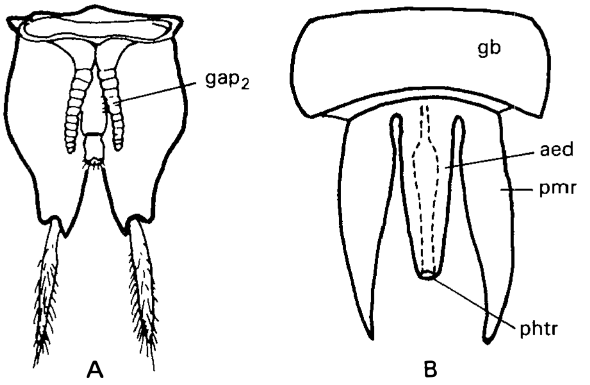


Figure 2–33 A, Male genitalia of Machilidae, ventral view; **B**, External genitalia of pterygotes (diagrammatic). *aed*, aedeagus; *gap*$_2$, second gonapophysis; *pmr*, paramere; *phtr*, phallotreme. (A, Redrawn from Snodgrass 1935, *Principles of Insect Morphology,* 1993, Cornell University Press; **B**, Redrawn from Snodgrass 1951.)

talia of silverfish and bristletails are not involved with copulation. In these insects as well as the entognathous hexapods, sperm transfer is indirect: The male places his spermatophore or a sperm droplet on the substrate, and the female actively places it in her gonopore. The penis of lepismatids is used to spin a silken web on which the spermatophore is placed.

There is considerable debate concerning the origin of the male genitalia in pterygotes. Some entomologists contend that they are derived from the appendages of segment 9 alone, and some include both these appendages and the penis of segment 10 (as seen in machiloids and lepismatoids). Snodgrass (1957) held that the genitalia are derived from outgrowths of sternum 10. In very general terms, the genitalia consist of outer clasping organs and a median intromittant organ (Figure 2–33B). The outer claspers, or **parameres** (pmr), may arise from a common base, the **gonobase** or **basal ring** (gb). The median intromittant organ is the **aedeagus** (aed). The opening of the aedeagus through which the spermatophore or the semen passes is the **phallotreme** (phtr). In many species, the ejaculatory duct is everted through the phallotreme during copulation; this eversible lining is called the *endophallus.* Such diversity exists in the structure and nomenclature of the male genitalia that it is beyond the scope of this book to describe them in more detail (see Tuxen 1970 for an order-by-order account of genitalic structure and the nomenclature used). This diversity of structure is very useful in identifying many groups of insects at the species level; such identification usually requires dissection and mounting of the genitalia for closer study.

Development and Metamorphosis

Sex Determination

The chromosomes of insects (as well as other animals) usually occur in pairs, but in one sex the members of one pair do not match or are represented by one chromosome only. The chromosomes of this odd pair are called *sex chromosomes;* those of the other pairs, *autosomes.* In most insects, the males has just one X (sex) chromosome (and is called *heterogametic*) and the female has two (*homogametic*). The male condition is generally referred to as XO (if only one chromosome in this pair is present) or XY (the Y chromosome being different in size or shape from the X chromosome), and the female as XX (two X chromosomes). One major exception to this generalization is in the Lepidoptera; in most species in this order, it is the female that is heterogametic (the WZ/ZZ system, females are WZ, males ZZ).

The autosomes appear to contain genes for "maleness," while the X chromosomes contain genes for "femaleness." More accurately, it seems the sex is determined by the balance between these two groups of genes. With two autosomes of each pair and only one X chromosome, the genes for maleness predominate and the animal becomes a male. With two autosomes of each pair and two X chromosomes, the genes for femaleness predominate and the animal becomes a female.

Sex is determined a little differently in the Hymenoptera and a few other insects. In these insects, the males are generally haploid (only very rarely diploid), and the females are diploid. The males develop from unfertilized eggs and the females develop from fertilized eggs (a type of parthenogenesis called *arrhenotoky*). Just how a haploid condition produces a male and a diploid condition produces a female is less well understood, but geneticists believe that sex in these insects depends on a series of multiple alleles (*Xa, Xb, Xc,* and so on): haploids and homozygous diploids (*Xa/Xa, Xb/Xb, Xc/Xc,* and so on) are males, while heterozygous diploids (*Xa/Xb, Xc/Xd,* and so on) only are females.

Parthenogenetic development producing females occurs in many insects (this type is called *thelytoky*). In some of these species, males are relatively rare or are unknown. These insects usually have the XO or XY male and XX female sex-determining mechanism, which means that either the eggs fail to undergo meiosis and are diploid or they do undergo meiosis and two cleavage nuclei fuse to restore the diploid condition. Some insects (for example, gall wasps and aphids) produce both males and females parthenogenetically (at certain seasons). The production of a male apparently involves the loss of an X chromosome, and the production of a female involves either a fusion of two cleavage nuclei to restore the diploid condition or diploid eggs arising from tetraploid germ tissue.

Recent research has revealed the widespread presence of the bacterium *Wohlbachia* in a great diversity of insects. In some cases, the bacterium kills embryos that would develop into males.

Individual insects sometimes develop with aberrant sex characters. Individuals having some male tissues and some female tissues are called *gynandromorphs;* such individuals sometimes occur in the Hymenoptera and Lepidoptera. In the Hymenoptera, where the sex-determining mechanism is haploidy = male and diploidy = female, a gynandromorph may develop from a binucleate egg in which only one of the nuclei is fertilized or may develop when an extra sperm enters the egg and undergoes cleavage to produce haploid (male) tissue in an otherwise female individual. Individuals with a sexual condition intermediate between maleness and femaleness are called *intersexes.* These usually result from genetic imbalance, particularly in polyploids (for example, a triploid *Drosophila* with an XXY sex chromosome content is an intersex and is sterile).

Eggs

The eggs of different insects vary greatly in appearance (Figures 2–34 through 2–36). Most eggs are spherical, oval, or elongate (Figure 2–34B,C,G), but some are barrel shaped (Figure 2–35), some are disk shaped, and

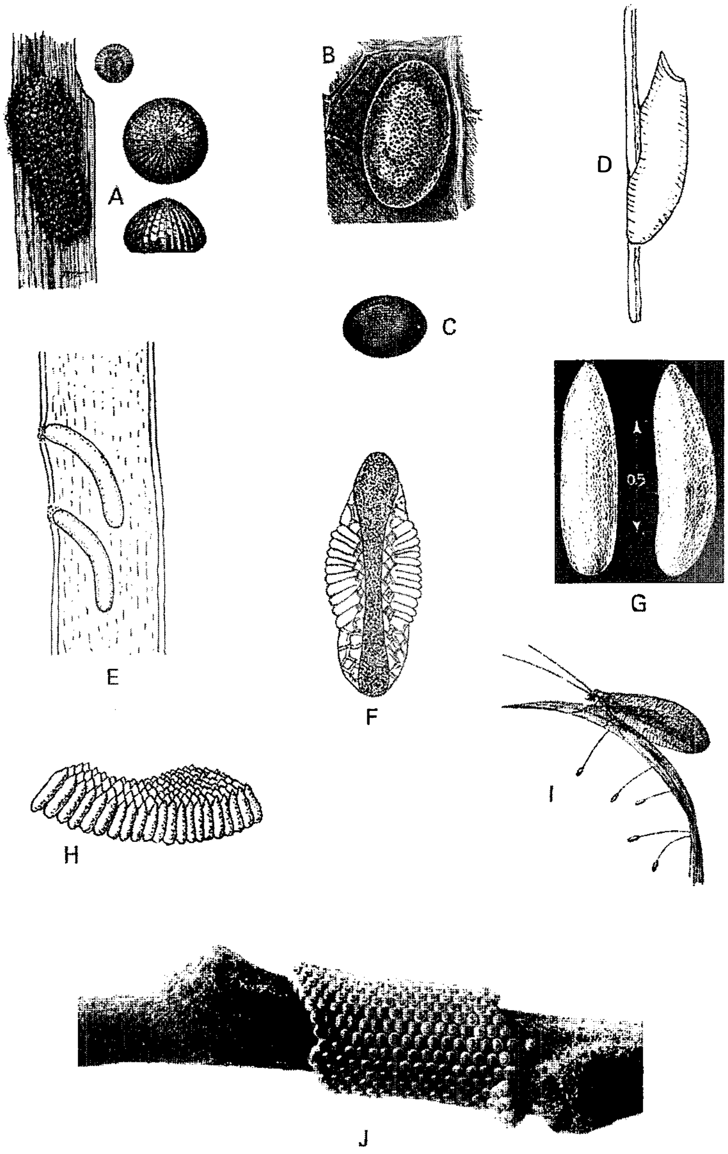
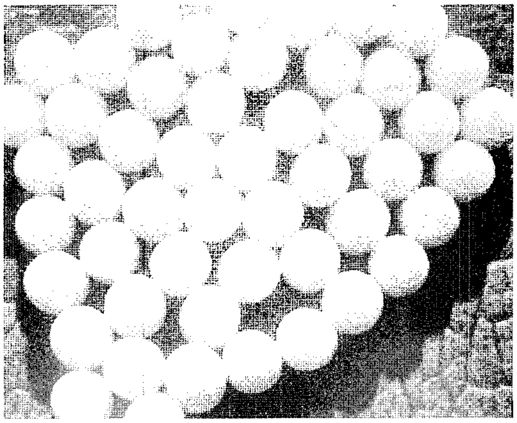
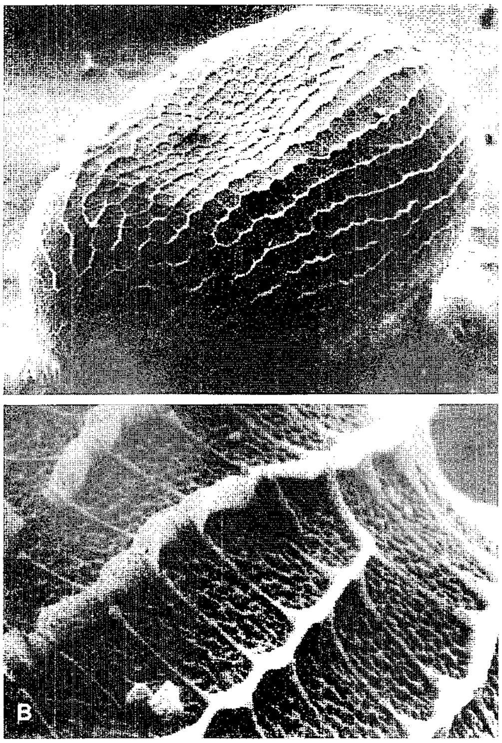


Figure 2–34 Insect eggs. A, Fall armyworm, *Spodoptera frugiperda* (J. E. Smith); **B**, Grape leaf-folder, *Desmia funeralis* (Hübner); C, Southern corn rootworm, *Diabrotica undecimpunctata howardi* Barber; **D**, Horse bot fly, *Gasterophilus intestinalis* (De Geer); **E**, Snowy tree cricket, *Oecanthus fultoni* Walker; **F**, *Anopheles* mosquito; G, Seedcorn maggot, *Hylemya platura* (Meigen); H, *Culex* mosquito, egg raft; **I**, Lacewing, *Chrysopa* sp.; **J**, Fall cankerworm, *Alsophila pometaria* (Harris). (A–C, **I**, courtesy of USDA; **J**, courtesy of Ohio Agricultural Research and Development Center.)



Ohio Agricultural Research and Development Center

Figure 2–35 Eggs of a stink bug.



Foster F. Purrington

Foster F. Purrington

Figure 2–36 Egg of a clearwing moth (Sesiidae). A, Egg of *Podosesia syringae* (Harris), 50×; B, Same, showing detail of egg surface, 290×. (Courtesy of the Ohio Agricultural Research and Development Center.)

so on. The egg is covered with a shell that varies in thickness, sculpturing, and color: Many eggs are provided with characteristic ridges, spines, or other processes, and some are brightly colored.

Most insect eggs are laid in a situation where they are afforded some protection or where the young, on hatching, will have suitable conditions for development. Many insects enclose their eggs in some sort of protective material. Cockroaches, mantids, and other insects enclose their eggs in an egg case or capsule. The tent caterpillars cover their eggs with a shellaclike material. The gypsy moth lays its eggs in a mass of its body hairs. Grasshoppers, june beetles, and other insects lay their eggs in the ground. Tree crickets insert their eggs in plant tissues (Figure 2–34E). Most plant-feeding insects lay their eggs on the food plant of the young. Insects whose immature stages are aquatic usually lay their eggs in or near water, often attaching them to objects in the water. Parasitic insects usually lay their eggs in or on the body of the host. Some insects deposit their eggs singly, whereas others lay their eggs in characteristic groups or masses (Figures 2–34H, J, and 2–35). The number laid varies from one in certain aphids to many thousands in some of the social insects, but most insects lay from 50 to a few hundred eggs.

Most insects are oviparous; that is, the young hatch from the eggs after they have been laid. In a few insects, the eggs develop within the body of the female, and living young are deposited. The extreme in this case is seen in the sheep ked, for example: The female fly retains the egg and larva within her body for an extended period of time. When parturition ("birth") finally occurs, the larva almost immediately burrows in the ground and pupates. Thus the only active feeding stage is the adult parasitic fly.

Embryonic Development

The egg of an insect is a cell with two outer coverings, a thin vitelline membrane surrounding the cytoplasm and an outer chorion. The chorion, which is the hard outer shell of the egg, has a minute pore or set of pores (the micropyle) at one end, through which sperm enter the egg (Figure 2–37A). Just inside the vitelline membrane is a layer of cortical cytoplasm. The central portion of the egg, inside the cortical cytoplasm, is largely yolk.

Most insect eggs undergo what is termed *superficial cleavage*. The early cleavages involve only the nucleus, giving rise to daughter nuclei scattered through the cytoplasm (Figure 2–37B). Eventually these nuclei migrate to the periphery of the egg (to the layer of cortical cytoplasm). After nuclear migration, the periph-

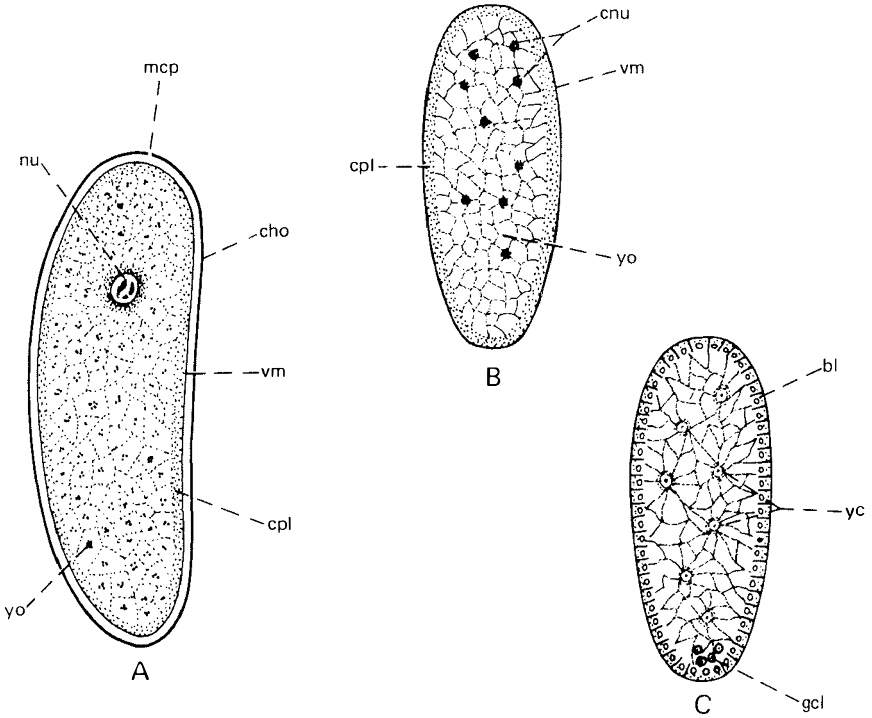


Figure 2–37 A, Diagram of a typical insect egg; B, Early cleavage; C, Peripheral blastoderm layer formed. *bl*, blastoderm; *cho*, chorion; *cnu*, cleavage nuclei; *cpl*, cortical cytoplasm; *gcl*, germ cells; *mcp*, micropyle; *nu*, nucleus; *vm*, vitelline membrane; *yc*, yolk cells; *yo*, yolk. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

eral cytoplasm becomes subdivided into cells, usually each with one nucleus, forming a cell layer, the blastoderm (Figure 2–37C, bl). This is the blastula stage. Within the blastoderm, in the mass of yolk material, are a few cells that do not take part in forming the blastoderm; these consist mainly of yolk cells.

The blastoderm cells on the ventral side of the egg enlarge and thicken, forming a germ band or ventral plate that will eventually form the embryo. The remaining cells of the blastoderm become the serosa and (later) the amnion. The germ band differentiates into a median area or middle plate and two lateral areas, the lateral plates (Figure 2–38A). The gastrula stage begins when the mesoderm is formed from the middle in one of three ways: by an invagination of this plate (Figure 2–38B,C), by the lateral plates growing over it (Figure 2–38D,E), or by a proliferation of cells from its inner surface (Figure 2–38F). Cells proliferate from each end of the mesoderm and eventually grow around the yolk. These cells represent the beginnings of the endoderm, and they form the lining of what will be the midgut of the insect (Figure 2–39). From the three germ layers—ectoderm, mesoderm, and endoderm—the various organs and tissues of the insect develop: the ectoderm gives rise to the body wall, tracheal system, nervous system, Malpighian tubules, and anterior and posterior ends of the alimentary tract; the mesoderm gives rise to the muscular system, heart, and gonads; the endoderm develops into the midgut.[3]

The alimentary tract is formed by invaginations from each end of the embryo, which extend to and unite with the primitive midgut (Figure 2–39). The anterior invagination becomes the foregut, the posterior invagination becomes the hindgut, and the central part (lined with endoderm) becomes the midgut. The cells lining the foregut and hindgut are ectodermal in origin and secrete cuticle.

Body segmentation becomes evident fairly early in embryonic development, appearing first in the anterior part of the body. It involves ectoderm and mesoderm,

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[3] Note that these embryonic tissues, in particular, the so-called endoderm, may not be homologous to that of deuterostomes.

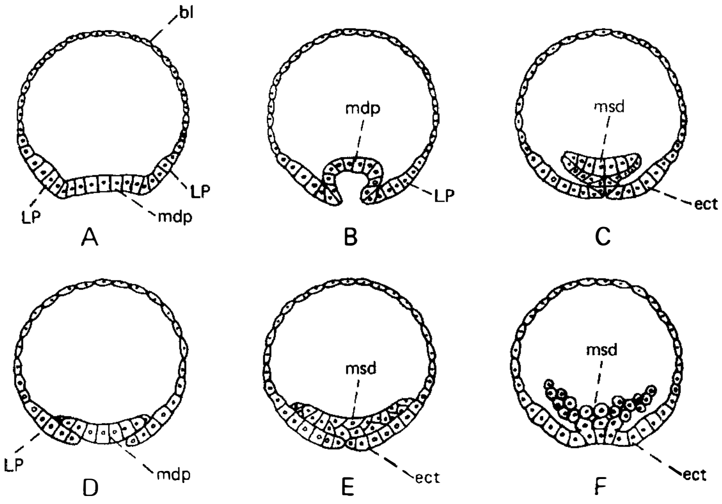

Figure 2–38 Cross-section diagrams showing mesoderm formation in insects. A, Germ band differentiated into middle and lateral plates; B, C, Stages in mesoderm formation by invagination of middle plate; D, E, Stages in mesoderm formation by lateral plates growing over middle plate; F, Mesoderm formation by internal proliferation from middle plate. *bl*, blastoderm; *ect*, ectoderm; *mdp*, middle plate; *LP*, lateral plate; *msd*, mesoderm. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

but not endoderm, and is reflected in the segmental arrangement of the structures developing from these germ layers (nervous system, heart, tracheal system, and appendages). The appendages appear soon after segmentation becomes evident. Typically, each segment begins to develop a pair of appendages, but most of these are resorbed and do not develop further.

The molecular mechanisms governing the pattern of development in embryos is a particularly active area of research. The initial orientation of the embryo is mediated by proteins derived from maternal RNA in the egg. Subsequently, a hierarchy of genes are transcribed that define the segmentation pattern in the embryo. Of particular interest are the homeobox genes, or HOX genes. In the insects that have been studied, there are eight HOX genes. In *Drosophila,* these are all located on chromosome 3 and occur in the order lab, pb, dfd, scr, antp, ubx, abd-A and abd-B. These abbreviations stand for *labial, proboscidea, deformed, sex combs reduced, antennapedia, ultrabithorax, abdomen-A,* and *abdomen-B.* These genes are differentially expressed in the embryo, both in space and time, and are crucial to defining segments and in the subsequent differentiation of limbs. They may well have further developmental roles that have not yet been clearly defined. The interest, from an evolutionary point of view, arises because very similar genes are found in distantly related phyla, implying an ancient evolutionary origin. Further, the expression of these genes and their enhancers have provided further tests of hypotheses concerning the homology of structures, for example, the mandibles in Crustacea, Myriapoda, and Hexapoda.

At some time early in its development, the embryo becomes surrounded by two membranes, an inner amnion and an outer serosa. Later it acquires a cuticular

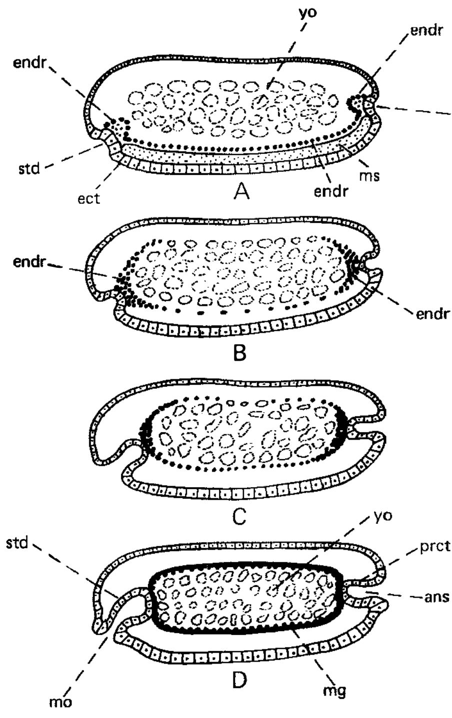

Figure 2–39 Diagrams showing the formation of the alimentary canal. A, Early stage in which the endoderm is represented by rudiments; B, C, Development of endoderm around yolk; D, Completion of alimentary canal. *ans*, anus; *ect*, ectoderm; *endr*, endodermal rudiments; *mg*, midgut; *mo*, mouth; *ms*, mesoderm; *prct*, proctodaeum; *std*, stomodaeum or foregut; *yo*, yolk. (Redrawn from Snodgrass 1935, *Principles of Insect Morphology*, 1993, Cornell University Press.)

membrane secreted by the epidermis. The formation of the amnion and serosa sometimes involves a reversal of position of the embryo in the egg; the embryo turns tail first into the yolk, away from the blastoderm. This turning carries part of the extraembryonic blastoderm into the yolk, and when the turning is complete, the opening into the embryonic cavity is closed. The extraembryonic blastoderm thus forms a lining (the amnion) around the embryonic cavity, and the outer part of the blastoderm, which surrounds the egg, becomes the serosa. The embryo later returns to its original position on the ventral side of the egg. In other cases the amnion and serosa are formed by folds of the blastoderm, which grow out from the edge of the germ band and unite beneath it. These membranes usually disappear before the embryo is ready to leave the egg. Cuticular coverings of the embryo (sometimes called *pronymphal membranes*) occur in insects with simple metamorphosis and in a few with complete metamorphosis. These are shed, by a process akin to molting, before or very shortly after hatching.

A young insect may escape from the egg in various ways. Most insects with mandibulate mouthparts chew their way out of the egg. Many insects have what are called *egg-bursters*: spinelike, knifelike, or sawlike processes on the dorsal side of the head—which are used in breaking through the eggshell. The eggshell is sometimes broken along weakened lines, either by the wriggling of the insect within or by the insect taking in air and rupturing the shell by internal pressure. The hatching from the egg is called *eclosion*.

Polyembryony is the development of two or more embryos from a single egg. It occurs in some of the parasitic Hymenoptera and in the Strepsiptera. In the embryonic development of such an insect, the dividing nucleus forms cell clusters, each of which develops into an embryo. The number of embryos that grow to maturity in a given host depends on the relative sizes of the parasite larvae and the host. In some cases, there are more parasite larvae than the food supply (the body contents of the host) can support, and some of them die and may be eaten by the surviving larvae. The number of young from a single egg varies in *Macrocentrus* (Braconidae) from 16 to 24, but in *M. ancylivorus* Rohwer only one parasite larva leaves the host. In *Platygaster* (Platygastridae) from 2 to 18 larvae develop from a single egg, and in *Aphelopus* (Dryinidae) from 40 to 60 develop from a single egg; in some of the Encyrtidae, more than 1500 young develop from a single egg.

Postembryonic Growth

Having an exoskeleton presents a problem as far as growth is concerned. To function as an exoskeleton, the insect's body wall must be relatively rigid, but if it is rigid, it cannot expand very much. Therefore, as the insect grows or increases in size, the exoskeleton must be periodically shed and replaced with a larger one. The process of digesting portions of the old cuticle and synthesizing the new cuticle is called *molting* (also spelled *moulting*), which culminates in the shedding of the old cuticle (ecdysis).

The molt involves not only the cuticle of the body wall but also the cuticular linings of the tracheae, foregut, and hindgut and the endoskeletal structures. The tracheal linings usually remain attached to the body wall when it is shed. The linings of the foregut and hindgut usually break up, and the pieces are passed out through the anus. The tentorium usually breaks into four pieces, which are withdrawn through the tentorial pits during the molt. The cast skins, called *exuviae*, often retain the shape of the insects from which they were shed.

The initial stages in the molting cycle are triggered by the release of PTTH (brain hormone) from neurosecretory cells in the brain. This stimulates the prothoracic glands (also sometimes called the *molting glands*) to release ecdysone into the hemolymph. Ecdysone, in turn, stimulates the separation of the old cuticle from the underlying epidermis, a process known as *apolysis*. The epidermis undergoes mitosis and grows in size; after this, the new cuticle is produced. Molting fluid secreted from the epidermal cells contains enzymes that digest the old endocuticle (but do not affect the epicuticle or exocuticle), and as a new cuticle is being deposited, the digestive products are resorbed into the body. Once this new exoskeleton is complete, the insect is ready to shed or break out of the old one. Ecdysis is triggered by a molting hormone, and begins with a splitting of the old cuticle along lines of weakness, usually in the midline of the dorsal side of the thorax. The rupturing force is pressure of the hemolymph (and sometimes air or water), forced into the thorax by contraction of the abdominal muscles. This split in the thorax grows, and the insect eventually wriggles its way out of the old cuticle.

When it first emerges from the old cuticle, the insect is pale in color, and its cuticle is soft. Within an hour or two, the exocuticle begins to harden and darken. During this brief period, the insect enlarges to the size of that instar, usually by taking in air or water. The wings (if present) are expanded by forcing hemolymph into their veins. The alimentary tract often serves as a reservoir of the air used in this expansion: If the crop of a cockroach, for example, is punctured with a needle, the insect does not expand but collapses; if the wing tips of an emerging dragonfly are cut off, hemolymph escapes from the cut end and the wings fail to expand. In addition to allowing the cuticle to expand, this period between ecdysis and hardening of the cuticle allows insects that pupate in the soil, for example, to crawl to the surface, there to expand the cuticle. In some species, researchers have identified a proteinaceous hormone, bursicon, that controls the process of sclerotization.

The number of molts varies among most insects from 4 to 8, but some of the Odonata undergo 10 or 12 molts, and some of the Ephemeroptera may undergo as many as 28 molts. A few hexapods, such as the entognathous orders, silverfish, and bristletails, continue to molt after reaching the adult stage, but winged insects neither molt nor increase in size once the adult stage is reached. (Mayflies have a sexually immature winged instar preceding the adult, the subimago, that molts.)

The stage of the insect between ecdyses is generally called an *instar.* The first instar is between hatching and the first larval or nymphal molt; the second instar is between the first and second molts; and so on. However, the full process of molting is not instantaneous. There is a period of time, usually short, but sometimes very long, between apolysis and ecdysis during which the next instar of the insect is "hidden" within the old cuticle. Hinton (1971) suggested that the term *instar* be used to refer to period of time from one apolysis to the next, and he proposed the term *pharate instar* to refer to the insect during the time between apolysis and ecdysis. In many cases this time period is sufficiently short that little confusion arises concerning which event signals the end of one instar and the beginning of the next. However, in some, such as the cyclorrhaphous Diptera, the distinction is important. In these flies, larval-pupal apolysis is not followed by an immediate ecdysis. Instead, the last larval cuticle is hardened to form a sort of cocoon within which lies the pharate pupa. Full development of the pupa is followed by the pupal-adult apolysis. The adult cuticle is then formed, and at that point ecdysis occurs with the adult fly shedding both the last larval and pupal cuticle at the same time.

The increase in size at each molt varies in different species and in different body parts and can be influenced by a number of environmental conditions. In many insects, however, the increase generally follows a geometric progression. The increase in the width of the larval head capsule in Lepidoptera, for example, is often a factor of 1.2 to 1.4 at each molt (Dyar's rule). In species where the individual molts are not actually observed, Dyar's rule can sometimes be applied to head capsule measurements of a series of different-sized larvae to estimate the number of instars.

Metamorphosis

Most insects change in form during postembryonic development, and the different instars are not all alike. This change is called *metamorphosis.* Some insects undergo very little change in form, and the young and adults are very similar except for size (Figures 2–40 and 2-41). In other cases the young and adults are quite different, in habits as well as in form (Figure 2–42).

There is quite a bit of variation in the metamorphosis occurring in different insect groups, but these variations can be roughly grouped into two general types: simple metamorphosis and complete metamorphosis. In simple metamorphosis, the wings (if any) develop externally during the immature stages, and there is ordinarily no quiescent stage preceding the last molt (Figures 2–40 and 2–41). In complete metamorphosis, the wings (if any) develop internally during the immature stages, and a quiescent or pupal stage normally precedes the last molt (Figure 2–42). The pupal stage is quiescent in that the insect at this time ordinarily does not move around, but a very considerable amount of change (to the adult) is taking place in this stage.

The changes during metamorphosis are accomplished by two processes, histolysis and histogenesis. Histolysis is a process whereby larval structures break down into material that can be used in developing adult structures. Histogenesis is the process of developing the adult structures from the products of histol-

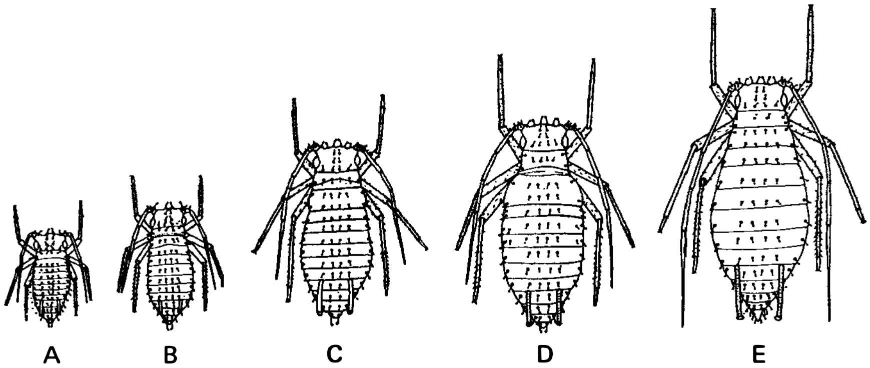

Figure 2–40 Stages in the development of the strawberry aphid, *Chaetosiphon fragaefolii* (Cockerell). A, First instar; B, Second instar; C, Third instar; D, Fourth instar; E, Adult female. (Courtesy of Baerg and Arkansas Agricultural Experiment Station.)

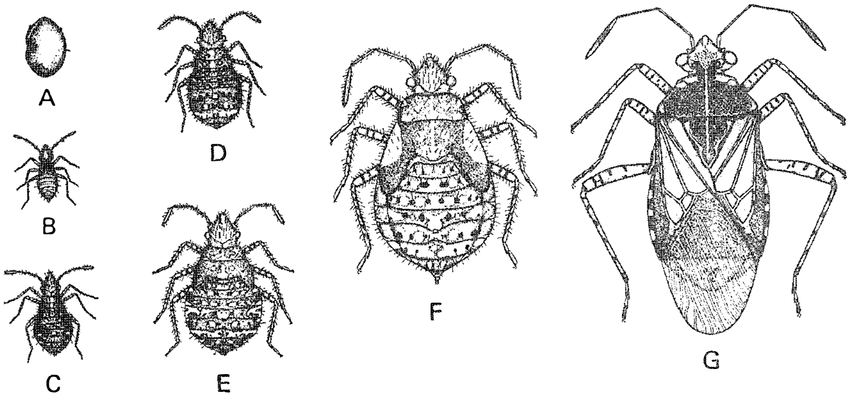

Figure 2–41 Stages in the development of the grass bug, *Arhyssus sidae* (Fabricius). A, Egg; B, First instar; C, Second instar; D, Third instar; E, Fourth instar; F, Fifth instar; G, Adult female. (Courtesy of Readio 1928 and the Entomological Society of America.)

ysis. The chief sources of material for histogenesis are the hemolymph, fat body, and histolyzed tissues such as larval muscles. Ectodermal structures, such as wings and legs, develop beneath the larval cuticle as epidermal thickenings called *imaginal discs.* These tissues respond quite differently from other larval tissues to the hormonal milieu of the insect. In the late larval instars, these tissues are elaborated to form the adult structures, and when the insect pupates, they are everted (hence one name for holometabolous insects, the Endopterygota, referring to the development of the wings inside the body of the larva). Other organs may be retained from the larva to the adult or may be completely rebuilt from regenerative cells.

Simple Metamorphosis

The young of insects with this type of metamorphosis are called *nymphs*[4] and are usually very similar to the adults. If compound eyes are present in the adult, they are present in the nymph. If the adults are winged, the wings appear as budlike outgrowths in the early instars (Figure 2–41) and increase in size only slightly up to the last molt. After the last molt, the wings expand to their full adult size. Simple metamorphosis occurs in the hexapod orders 1 to 22 (see list, Chapter 6).

Differences in the kind and amount of change occur in the insects with simple metamorphosis, and some entomologists recognize three types of metamorphosis in these insects: ametabolous, paurometabolous, and hemimetabolous. Ametabolous insects (with "no" metamorphosis) are wingless as adults, and the only obvious difference between nymphs and adults is size. This type of development occurs in the apterygote orders (Protura, Collembola, Diplura, Microcoryphia, and Thysanura) and in most wingless members of the other orders with simple metamorphosis. In hemimetabolous metamorphosis (with "incomplete" metamorphosis), the nymphs are aquatic and gill-breathing and differ considerably from the adults in appearance. This type of development occurs in the Ephemeroptera, Odonata, and Plecoptera, and the young of these insects are sometimes called *naiads.* Paurometabolous insects (with "gradual" metamorphosis) include the remaining insects with simple metamorphosis. The adults are winged; the nymphs and adults live in the same habitat; and the principal changes during growth are in size, body proportions, the development of the ocelli, and occasionally the form of other structures.

Complete Metamorphosis

The immature and adult stages of insects that undergo complete metamorphosis are usually quite different in form, often live in different habitats, and have very different habits. The early instars are often more or less wormlike, and the young in this stage are called *larvae* (Figures 2–42 and 2–43). The different larval instars are usually similar in form but differ in size. The wings, when they are present in the adult, develop internally during the larval stage and are not everted until the end of the last larval instar. Larvae generally have chewing mouthparts, even in those orders in which the adults have sucking mouthparts.

Following the last larval instar, the insect transforms into a stage called the *pupa* (Figure 2–44). The insect does not feed in this stage and is usually inactive. Pupae are often covered by a cocoon or some other protective material, and many insects pass the winter in the pupal stage. The final molt occurs at the end of the pupal stage, and the last stage is the adult.

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[4] In the European literature of entomology, the immature stages of all insects are generally referred to as *larvae.*

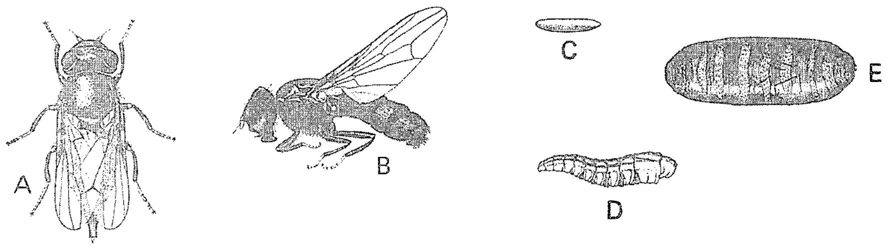

Figure 2–42 Stages in the development of the sugarbeet root maggot, *Tetanops myopaeformis* (Röder). A, Adult female; B, Adult male; C, Egg; D, Larva; E, Puparium (pupa inside). (From Knowlton 1937, used courtesy of the Utah Agricultural Experiment Station.)

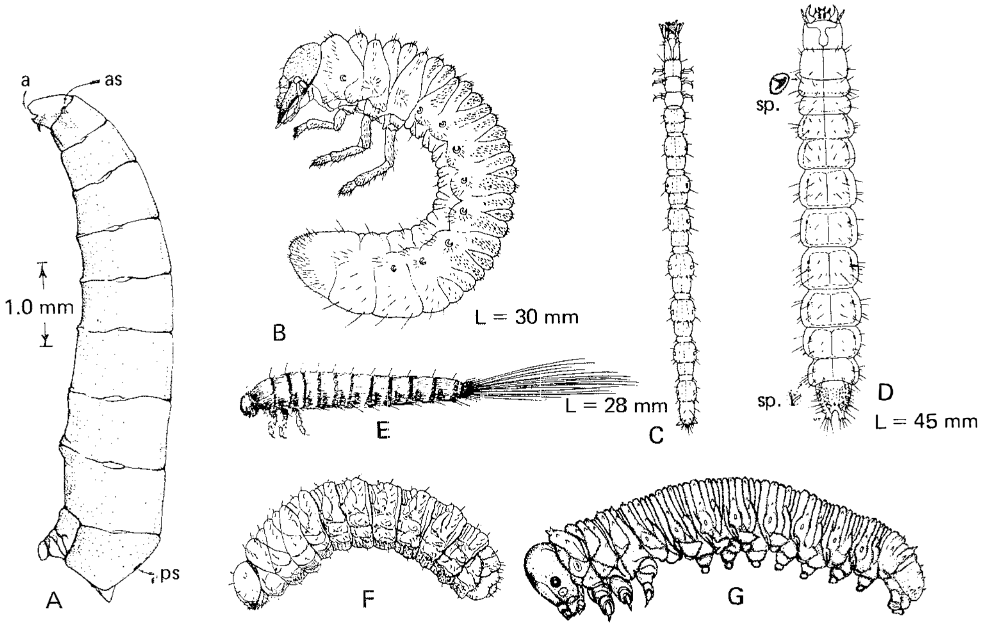

Figure 2–43 Insect larvae. A, Maggot or vermiform larva of *Hylemya platura* (Meigen) (Diptera, Anthomyiidae); B, Grub or scarabaeiform larva of *Phyllophaga rugosa* (Melsheimer) (Coleoptera, Scarabaeidae); C, Elateriform larva of *Cardiophorus* sp. (Coleoptera, Elateridae); D, Elateriform larva of *Alaus oculatus* (L.) (Coleoptera, Elateridae); E, Campodeiform larva of *Attagenus megatoma* (Fabricius) (Coleoptera, Dermestidae); F, Vermiform larva of *Cylas formicarius elegantulus* (Summers) (Coleoptera, Brentidae); G, Eruciform larva of *Caliroa aethiops* (Fabricius) (Hymenoptera, Tenthredinidae). *a*, antenna; *as*, anterior spiracle; *L*, length; *ps*, posterior spiracle; *sp*, spiracle. (A, E–G, Courtesy of USDA; B–D, From Peterson, 1948, by permission.)

The adult is usually pale in color when it first emerges from the pupa, and its wings are short, soft, and wrinkled. In a short time, from a few minutes to several hours or more, depending on the species, the wings expand and harden, the pigmentation develops, and the insect is ready to go on its way. This type of metamorphosis, which occurs in orders 23 to 31, is often called *holometabolous* (see list, Chapter 6), and these orders are classified together as the Holometabola.

Hypermetamorphosis is a type of complete metamorphosis in which the different larval instars are not of the same type. The first instar is active and usually campodeiform, and the subsequent larval instars are vermiform or scarabaeiform (see definitions of these

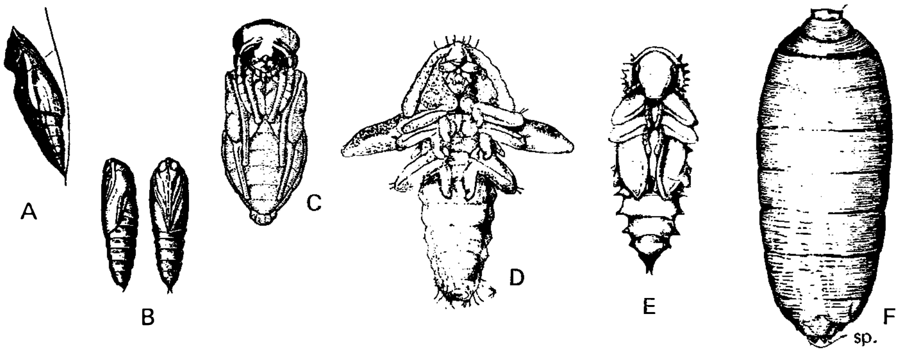

Figure 2–44 Insect pupae. A, Chrysalis of the sulphur butterfly, *Colias eurytheme* Boisduval (Lepidoptera, Pieridae); B, Fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera, Noctuidae); C, Clover seed chalcid, *Bruchophagus platyptera* (Walker) (Hymenoptera, Eurytomidae); D, Sweetpotato weevil, *Cylas formicarius elegantulus* (Summers) (Coleoptera, Brentidae); E, Sawtoothed grain beetle, *Oryzaephilus surinamensis* (L.) (Coleoptera, Silvanidae); F, Seedcorn maggot, *Hylemya platura* (Meigen) (Diptera, Anthomyiidae). A and B are obtect pupae, C–E are exarate pupae, and F is a coarctate pupa. (Courtesy of USDA.)

terms later). Hypermetamorphosis occurs in parasitic insects; the first instar seeks out the host and, once in the host, molts into a less active type of larva. This type of complete metamorphosis occurs in the Meloidae (Figure 26-68) and Ripiphoridae (Coleoptera), the Mantispidae (Neuroptera), the Strepsiptera, and a few Diptera and Hymenoptera.

Intermediate Types of Metamorphosis

Not all insects have a type of metamorphosis that can be readily classified as simple or complete. Some have a metamorphosis that is somewhat intermediate between these two types. Such metamorphosis is found in thrips (Chapter 23), whiteflies (Chapter 22), and male scale insects (Chapter 22). In fact, these groups have gone far toward evolving complete metamorphosis independently of the orders just discussed.

The first two instars of thrips (Thysanoptera) are wingless and active and are usually called *larvae*. The next two instars (the next three in the suborder Tubulifera) are inactive, with external wings. The first of these (the first two in Tubulifera) is called a *prepupa*, and the last a *pupa*. The final instar is the adult. Apparently at least some of the wing development is internal during the first two instars. This metamorphosis resembles complete metamorphosis in that at least some of the wing development is internal, and an inactive, "pupal" stage precedes the adult. It is similar to simple metamorphosis in that the early instars have compound eyes, and external wing buds are present in more than one preadult instar.

Whiteflies have five instars, the last of which is the adult. The first instar is active and wingless, and the next three instars are inactive, sessile, and scalelike, with the wings developing internally. The fourth instar, called the *pupa*, has external wings. The first three instars are usually called *larvae*. The molt from the last larval instar to the pupa takes place inside the last larval skin, which forms the puparium. This metamorphosis is essentially complete, although most other members of this order (Hemiptera) have simple metamorphosis.

The males of scale insects have a type of metamorphosis that is very similar to that in whiteflies. The first instar (Figure 22-63B), the "crawler," is active and wingless, but the remaining preadult instars are sessile and inactive. The last preadult instar, which has external wings, is called the *pupa*. The development of wings is at least partly internal.

Control of Metamorphosis

The metamorphosis of insects is controlled by three hormones: PTTH (prothoracicotropic or brain hormone), ecdysone, and JH (juvenile hormone). PTTH is produced by neurosecretory cells in the brain and stimulates the prothoracic glands (also known as the *molting glands*) to produce ecdysone, which induces apolysis and promotes growth. JH is produced by cells in the corpora allata and inhibits metamorphosis, thereby promoting further larval or nymphal development. Removing JH from a larva or nymph (by removing the corpora allata) causes the larva to pupate and the nymph to develop into an adult when ecdysone is present. Injection of juvenile hormone into a pupa (in the presence of ecdysone) will cause the pupa to develop into a second pupa. Injecting JH into a last-instar nymph or larva causes another nymphal or larval stage to be produced at the next molt. The corpora allata are active during the early instars and usually cease secreting JH in the last pre-adult instar. The absence of the hormone in this instar results in metamorphosis.

The changes from instar to instar in insects with simple metamorphosis are generally relatively slight and gradual, being most marked at the final molt to the adult, but insects with complete metamorphosis show considerable reorganization within the insect in the pupal stage. Some structures in the larva, such as the heart, nervous system, and tracheal system, change very little at metamorphosis. Other adult structures are present in a rudimentary form in the larva and remain so during successive larval instars. Then, more or less suddenly, they develop to their adult form in the pupal stage. Still other adult structures are not represented in the larva and must be developed at the time of metamorphosis.

Types of Larvae

The larvae of insects that undergo complete metamorphosis differ considerably in form, and several types have been recognized:

Eruciform—caterpillar-like (Figure 2–43G); body cylindrical, the head well developed but with very short antennae, and with both thoracic legs and abdominal prolegs. This type occurs in the Lepidoptera, Mecoptera, and some Hymenoptera (suborder Symphyta).

Scarabaeiform—grublike (Figure 2–43B); usually curved, the head well developed, with thoracic legs but without abdominal prolegs, and relatively inactive and sluggish. This type occurs in certain Coleoptera (for example, Scarabaeidae).

Campodeiform—resembling diplurans in the genus *Campodea* (Figure 7-4A); body elongate and somewhat flattened, the cerci and antennae usually well developed, the thoracic legs well developed, and the larvae usually active. This type occurs in the Neuroptera, Trichoptera, and many Coleoptera.

Elateriform—wirewormlike (Figure 2–43C,D); body elongate, cylindrical, and hard-shelled, the legs short, and the body bristles reduced. This type occurs in certain Coleoptera (for example, Elateridae).

Vermiform—maggotlike (Figure 2–43A,F); body elongate and wormlike, legless, and with or without a well-developed head. This type occurs in the Diptera, Siphonaptera, most Hymenoptera (suborder Apocrita), and some Coleoptera and Lepidoptera.

Types of Pupae

The pupae of insects with complete metamorphosis vary, and five types may be recognized:

Obtect—with the appendages more or less glued to the body (Figure 2–44A,B). This type occurs in the Lepidoptera and some Diptera (suborder Nematocera). The pupa in many Lepidoptera is covered by a silken cocoon formed by the larva before it molts to the pupal stage.

Exarate—with the appendages free and not glued to the body (Figure 2–44C-E). Such a pupa looks much like a pale, mummified adult and is usually not covered by a cocoon. This type occurs in most insects with complete metamorphosis, except the Diptera and Lepidoptera.

Coarctate—essentially like an exarate pupa, but remaining covered by the hardened cuticle of the last larval instar, which is called a *puparium* (Figure 2–44F). This type occurs in the Diptera (suborder Brachycera).

Decticous—with the mandibles movably articulated with the head. This type is also always exarate and occurs in the Neuroptera, Trichoptera, and some Lepidoptera.

Adecticous—with the mandibles immovably attached to the head. This type of pupa is found in the remaining groups of holometabolous insects.

Variations in Life History

The length of a generation and the way it is fitted to the different seasons vary quite a bit in different insects. Most insects in temperate regions have what entomologists call a "heterodynamic life cycle"; that is, the adults appear for a limited time during a particular season, and some life stage passes the winter in a state of dormancy. The overwintering stage may be the egg (for example, most Orthoptera and Hemiptera), nymph (for example, most Odonata and many Orthoptera), larva (for example, many Lepidoptera), or adult (for example, most Hemiptera and many Coleoptera and Hymenoptera). Many insects, particularly those living in the tropics, have a homodynamic life cycle; that is, development is continuous and there is no regular period of dormancy.

Most insects in the United States have a single generation a year. Some require 2 or more years to complete their life cycle, as is usually the case with large insects occurring in the northern part of the country. Some of the large beetles, dragonflies, and moths in the northern states and Canada require 2 or 3 years to complete their development. Probably the longest life cycle of any insect is that of some of the periodical cicadas (*Magicicada* spp.), which lasts 17 years (see Chapter 22).

Many insects have more than one generation a year. In some cases, the number of generations in a year is constant throughout the range of the species. In other cases, the species may have more in the southern part of its range. A few insects, usually rather small species that can complete their life cycle in a few weeks, have many generations a year. Such insects continue to reproduce through the season as long as weather conditions are favorable. Insects of tropical origin, such as those of the household and those which attack stored products, may continue breeding throughout the entire 12 months.

In many insects, development is arrested during a specific stage of the annual cycle. This period of genetically programmed (that is, predetermined) dormancy is known as *diapause,* in contrast to periods of quiescence in response to adverse environmental conditions. A period of winter dormancy in temperate or arctic regions is often called *hibernation,* and a period of dormancy during high temperatures is called *aestivation.*

Diapause in insects is genetically controlled, and both onset and termination may be induced by environmental factors such as photoperiod or temperature. The chief factor initiating diapause seems to be photoperiod (day length). Studies of hornworm larvae (Sphingidae) have shown that all individuals that enter the soil for pupation before a certain date will complete their development, emerge as moths, and reproduce, but individuals entering the soil after this date go into diapause and do not complete their development until the following spring. This factor of day length apparently operates similarly in the case of the codling moth. Individuals of the first generation pupate and emerge as adults in the summer, but individuals of the second generation (in autumn) do not. In some cases (for example, *Antheraea,* family Saturniidae), day length may also control emergence from diapause. The larvae of the second generation of the codling moth in Ohio remain as diapausing larvae in silk-lined cells under the bark of apple trees unless subjected to a short period (some three weeks) of low temperatures (0°C or lower). When then returned to normal developmental temperatures, they pupate and complete their development. The effect of day length is usually direct, on the insect itself, but may occasionally be indirect, its effect being on the food eaten by the insect. Photoperiod may also be an important cue for the initiation of diapause in tropical insects, even though the changes in day length are much smaller than in temperate regions. Diapause in tropical insects may be associated with alternating wet and dry seasons, high temperatures, or the availability of appropriate food, instead of the avoidance of winter (Denlinger 1986).

References

Altner, H., and R. Loftus. 1985. Ultrastructure and function of insect thermo- and hygroreceptors. Annu. Rev. Entomol. 30:273–295.

Anderson, D. T. 1973. Embryology and Phylogeny in Annelids and Arthropods. New York: Pergamon Press, 495 pp.

Arms, K., and P. S. Camp. 1987. Biology. Philadelphia: Saunders College Publishing, 1142 pp.

Chapman, R. F. 1982. The Insects: Structure and Function, 3rd ed. Cambridge, MA: Harvard University Press, 919 pp.

Commonwealth Scientific and Industrial Research Organization (CSIRO). 1970. The Insects of Australia. Carlton, Victoria: Melbourne University Press, 1029 pp.

Comstock, J. H., and J. G. Needham. 1898. The wings of insects. Amer. Nat. 32:43–48, 81–89, 231–257, 335–340, 413–424, 561–565, 768–777, 903–911.

Comstock, J. H., and J. G. Needham. 1899. The wings of insects. Amer. Nat. 33:117–126, 573–582, 845–860.

Daly, H. V., J. T. Doyen, and P. R. Ehrlich. 1978. An Introduction to Insect Biology and Diversity. New York: McGraw-Hill, 564 pp.

Davey, K. G. 1965. Reproduction in the Insects. San Francisco: Freeman, 96 pp.

Denlinger, D. L. 1986. Dormancy in tropical insects. Annu. Rev. Entomol. 31:239–264.

Dethier, V. G. 1963. The Physiology of Insect Senses. New York: Wiley, 266 pp.

Dethier, V. G. 1976. The Hungry Fly: A Physiological Study of Behavior Associated with Feeding. Cambridge, MA: Harvard University Press, 489 pp.

Eberhard, W. G. 1985. Sexual selection and animal genitalia. Cambridge, MA: Harvard University Press, 224 pp.

Ferris, G. F., and B. E. Rees. 1939. The morphology of *Panorpa nuptialis* Gerstaecker (Mecoptera: Panorpide). Microentomology 4:79–108.

Fox, R. M., and J. W. Fox. 1964. Introduction to Comparative Entomology. New York: Reinhold, 450 pp.

Gilbert, L. I. 1976. The Juvenile Hormones. New York: Plenum Press, 572 pp.

Gordh, G., and D. H. Headrick. 2001. A dictionary of entomology. Wallingford, Oxon, UK: CABI Publishing, 1050 pp.

Hepburn, H. R. (Ed.). 1976. The Insect Integument. New York: American Elsevier, 572 pp.

Hinton, H. E. 1955. On the structure, function, and distribution of the prolegs of the Panorpoidea, with a criticism of the Berlese-Imms theory. Trans. Roy. Entomol. Soc. Lond. 106:455–545.

Hinton, H. E. 1971. Some neglected phases in metamorphosis. Proc. Roy. Entomol. Soc. Lond. (C) 35:55–64.

Hinton, H. E. 1981. Biology of Insect Eggs. 3 vols. New York: Pergamon Press, 1125 pp.

Horn, D. J. 1976. Biology of Insects. Philadelphia: Saunders, 439 pp.

Horridge, G. A. (Ed.). 1975. The Compound Eye and Vision of Insects. New York: Clarendon Press, 595 pp.

Jacobson, M. 1972. Insect Sex Hormones. New York: Academic Press, 382 pp.

Jamieson, B. G. M. 1987. The Ultrastructure and Phylogeny of Insect Spermatozoa. Cambridge, UK: Cambridge University Press, 320 pp.

Jones, J. C. 1977. The Circulatory System of Insects. Springfield, IL: C. C Thomas, 255 pp.

Kerkut, G. A., and L. I. Gilbert (Eds.). 1985. Comprehensive Insect Physiology, Biochemistry and Pharmacology. 13 vols. Vol. 1: Embryogenesis and Reproduction; 482 pp. Vol. 2: Postembryonic Development; 505 pp. Vol. 3: Integument, Respiration and Circulation; 625 pp. Vol. 4: Regulation: Digestion, Nutrition, Excretion; 639 pp. Vol. 5: Nervous System: Structure and Motor Function; 646 pp.

Vol. 6: Nervous System: Sensory; 710 pp. Vol. 7: Endocrinology I; 564 pp. Vol. 8: Endocrinology II; 595 pp. Vol. 9: Behaviour; 735 pp. Vol. 10: Biochemistry; 715 pp. Vol. 11: Pharmacology; 740 pp. Vol. 12: Insect Control; 849 pp. Vol. 13: Cumulative Indexes; 314 pp. New York: Pergamon Press.

Knowlton, G. F. 1937. Biological control of the beet leafhopper in Utah. Proc. Utah Acad. Sci., Arts, Letters 14:111–139.

Kukalová-Peck, J. 1978. Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. J. Morphol. 156:53–126.

Kukalová-Peck, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. Can. J. Zool. 61:1618–1669.

Kukalová-Peck, J. 1985. Ephemeroid wing venation based on new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects. Can. J. Zool. 63:933–955.

Manton, S. M. 1977. The Arthropoda, Habits, Functional Morphology, and Evolution. Oxford, UK: Clarendon Press, 527 pp.

Matheson, R. 1951. Entomology for introductory courses. Ithaca, NY: Comstock Publishing Company, Inc., 600 pp.

Matsuda, R. 1970. Morphology and evolution of the insect thorax. Mem. Entomol. Soc. Can. No. 76; 431 pp.

Matsuda, R. 1976. Morphology and Evolution of the Insect Abdomen, with Special Reference to Developmental Patterns and Their Bearing on Systematics. New York: Pergamon Press, 532 pp.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1981. Manual of Nearctic Diptera, vol. 1. Ottawa: Research Branch, Agricultural Canada Monograph No. 27, 674 pp.

Menn, J. J., and M. Beroza (Eds.). 1972. Insect Juvenile Hormones, Chemistry and Action. New York: Academic Press, 341 pp.

Nachtigall, W. 1968. Insects in Flight (translated from German by H. Oldroyd, R. H. Abbott, and M. Biederman-Thorson). New York: McGraw-Hill, 153 pp.

Neville, A. C. 1975. Biology of the Arthropod Cuticle. New York: Springer, 450 pp.

Novak, V. J. A. 1975 (2nd ed.). Insect Hormones. New York: Halsted, 600 pp.

Paulus, H. F. 1979. Eye structure and the monophyly of Arthropoda. *In* Arthropod Phylogeny, ed. A. P. Gupta, pp. 299-383. New York: Van Nostrand Reinhold, 762 pp.

Payne, T. L., M. C. Birch, and C. E. J. Kennedy (Eds.). 1986. Mechanisms in Insect Olfaction. Oxford, UK: Clarendon Press, 364 pp.

Peterson, A. 1948. Larvae of Insects. Part I. Lepidoptera and Hymenoptera. Ann Arbor, MI: Edwards, 315 pp.

Peterson, A. 1951. Larvae of Insects. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Ann Arbor, MI: Edwards, 416 pp.

Raabe, M. 1986. Insect reproduction: Regulation of successive steps. Adv. Ins. Physiol. 19:29–154.

Rainey, R. C. (Ed.). 1976. Insect Flight: Proceedings of a Symposium. New York: Halsted, 288 pp.

Readio, P. A. 1928. Studies on the biology of the genus *Corizus* (Coreidae: Hemiptera). Ann. Entomol. Soc. Amer. 21:189–201.

Rempel, J. G. 1975. The evolution of the insect head: The endless dispute. Quaest. Entomol. 11:7–25.

Riek, E. F., and J. Kukalová-Peck. 1984. A new interpretation of dragonfly wing venation based on Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. Can. J. Zool. 62:1150–1166.

Rockstein, M. (Ed.). 1973–1974. The Physiology of Insecta. 6 vols., illus. Vol. 1: Physiology of Ontogeny—Biology, Development, and Aging, 512 pp. (1973). Vol. 2: The Insect and the External Environment. Part A. I. Environmental Aspects. Part B. II. Reaction and Interaction, 517 pp. (1974). Vol. 3: The Insect and the External Environment. Part A. II. Reaction and Interaction. Part B. III. Locomotion, 517 pp. (1974). Vol. 4: The Insect and the External Environment. Homoeostasis I. 488 pp. (1974). Vol. 5: The Insect and the External Environment. Homoeostasis II. 648 pp. (1974). Vol. 6: The Insect and the External Environment. Homoeostasis III. 548 pp. (1974). New York: Academic Press.

Rodriguez, J. G. (Ed.). 1972. Insect and Mite Nutrition. New York: American Elsevier, 701 pp.

Roeder, K. D. 1967 (rev. ed.). Nerve cells and insect behavior. Cambridge, MA: Harvard University Press, 238 pp.

Romoser, W. S. 1973. The Science of Entomology. New York: Macmillan, 499 pp.

Rothschild, M., Y. Schlein, and S. Ito. 1986. A Colour Atlas of Insect Tissues via the Flea. London: Wolfe, 184 pp.

Sacktor, B. 1974. Biological oxidations and energetics in insect mitochondria. *In* Physiology of Insecta, ed. M. Rockstein, vol. 4, 271–353. New York: Academic Press.

Schwalm, F. 1988. Insect Morphogenesis. Monographs in Developmental Biology, vol. 20. New York: Karger, 356 pp.

Scudder, G. G. E. 1971. Comparative morphology of insect genitalia. Annu. Rev. Entomol. 16:379–406.

Snodgrass, R. E. 1935. Principles of Insect Morphology. New York: McGraw-Hill, 667 pp.

Snodgrass, R. E. 1952. A Textbook of Arthropod Anatomy. Ithaca, NY: Comstock, 363 pp.

Snodgrass, R. E. 1957. A revised interpretation of the external reproductive organs of male insects. Smithson. Misc. Coll. 135(6):1–60.

Stehr, F. (Ed.). 1987. Immature Insects. Dubuque, IA: Kendall/Hunt, 754 pp.

Tuxen, S. L. (Ed.). 1970. Taxonomist's Glossary of Genitalia in Insects. Copenhagen: Munksgaard, 359 pp.

Usherwood, P. N. R. 1975. Insect Muscle. New York: Academic Press, 622 pp.

Vogel, R. 1921. Kritische und ergänzeude Mitteilungen zur Anatomie des Stechapparats der Culiciden und Tabaniden. Zool. Jahrb. Anat. 42:259–282.

Wigglesworth, V. B. 1970. Insect Hormones. San Francisco: Freeman, 159 pp.

Wigglesworth, V. B. 1973 (7th ed.). The Principles of Insect Physiology. London: Methuen, 827 pp.

Wigglesworth, V. B. 1984 (8th ed.). Insect Physiology. New York: Chapman and Hall, 191 pp.

Wootton, R. J. 1979. Function, homology and terminology in insect wings. Syst. Entomol. 28:81–93.

3

Systematics, Classification, Nomenclature, and Identification

The theme of diversity inevitably dominates any discussion of insects and their relatives. Not only is there a large number of individual insects (the biomass of ants in the tropics probably exceeds that of all vertebrates combined), but there is an almost overwhelming number of different kinds of insects. The study of the diversity of organisms and of the relationships between them is the scientific field of **systematics**. This discipline also includes the study of classification, the field of **taxonomy**. Systematics forms the foundation on which all other biological disciplines rest. The names of organisms provide a key to the published literature and enable us to communicate with one another. Classifications serve both as information retrieval systems and, as they reflect the relationships among organisms, provide predictions of the distribution of characteristics among organisms.

The fundamental unit of systematics is the species. Concepts of what a species is and how they originate are based largely on studies of vertebrates. Extrapolation beyond them to other animals, especially to fundamentally different organisms in other kingdoms, must be done with some care. Basically, most researchers dealing with living animals define the species to be a group of individuals or populations in nature that (1) are capable of interbreeding and producing fertile offspring, and (2) under natural conditions are reproductively isolated from (that is, ordinarily not interbreeding with) other such groups. This is known as the *biological species concept*. Because these criteria involve characteristics of living organisms, they are difficult, sometimes perhaps impossible, to address directly. Therefore, the first steps in systematics usually involve attempts to infer the limits of a species (the extent of a reproductive community) by observing the phenotypic expression of that gene pool—to look for the smallest set of phenotypic homogeneity while acknowledging and incorporating known aspects of variability, such as sexual dimorphism, developmental stages, seasonal changes, geographic variation, and individual variability. Hence researchers often must rely on morphological or other characters to determine specific limits; caution is needed, because there are "good" species (groups reproductively isolated) that cannot be distinguished by morphological characters (known as *sibling species*), and conversely, within a single species there may be a number of different forms.

The subspecies category is sometimes used to refer to recognizable and geographically restricted populations of a species. Because different subspecies of a given species are capable of interbreeding, the differences between them are usually not clear-cut but intergrading, particularly where adjacent subspecies come in contact. This category has been misused, especially in the early part of the 20th century, to refer to any distinguishable variant, often a color variant.

Systematics

Classifications of insects and their relatives form the heart of this book. Classifications are tools that provide names for groups of species and serve as a shorthand for communicating information about those species. These instruments are utilitarian products that emerge from systematics, the study of the diversity and interrelationships of organisms. Although the field is as old as any area of biological inquiry, it has undergone a remarkable resurgence over the past two decades. This renaissance has been fueled by (1) theoretical advances in the nature and analysis of systematic data; (2) the development of new sources of data from nucleic acid sequences; (3) the development of powerful and affordable computers with which to analyze these data; and (4) the growth of the size and scope of natural history collections. As a result, the process that began approximately 50 years ago has now transformed the systematics from a field dominated by arcane facts and argument by authority, into a science driven by data, explicit hypotheses, and quantitative analysis. Nevertheless, systematics retains the aesthetic appeal that comes from the continual discovery of new, beautiful, sometimes bizarre, but always fascinating forms of life.

The conceptual advances in systematics were first coherently articulated by an entomologist, Willi Hennig, a specialist on Diptera. Hennig published his principles in German (Hennig 1950), but after publication in English his ideas received much more attention (Hennig 1965, 1966). He called this new approach *phylogenetic systematics;* today it is often referred to simply as phylogenetics or as cladistics. The ideas are fairly straightforward. The characters of a species are passed down from ancestor to descendant. Species, in general, do not interbreed; therefore characteristics in one species cannot be transferred to a different, parallel lineage. The appearance of new lineages, the process of speciation, involves splitting an ancestral species into two (or possibly more) descendant species. If a character changes, that is, becomes modified from its ancestral state, then this new, derived character will appear only in the species in which it arose or in its descendants. Therefore, the sequence of appearance of lineages through time can be reconstructed by documenting the distribution of derived characters.

As in any specialty, entomology has a fair amount of jargon that the student must understand. Derived characters are called apomorphies (even if the character is chemical, behavioral, or so on, and not morphological at all). The ancestral characters are referred to as plesiomorphies. Branches on the phylogenetic tree are hypothesized on the basis of shared derived characters among the species, called synapomorphies. Such groups are considered monophyletic (sometimes called *holophyletic*) groups and consist of an ancestral species and all its descendants. Shared ancestral characters are symplesiomorphies; groups defined on the basis of symplesiomorphies are paraphyletic. Unnatural groups, such as a group containing only insects and mosses, are polyphyletic. This is an extreme example, of course, but polyphyletic groups usually result from the misinterpretation of characters, such as thinking that two structures are "the same" when in fact they evolved independently in the species concerned. Thus the primary goal of phylogenetic systematics is the discovery of monophyletic groups.

These ideas that a structure found in two different species is the same structure and that they share it because they inherited the structure from their common ancestor constitute the definition of a homologous character. As you can see, the definitions of homologous characters and synapomorphies are equivalent. Characters that are not homologous, but only seem so, arise through the evolutionary processes of convergence, parallelism, and reversals. Convergence and parallelism are the development of similar structures independently in two different species. A reversal is a character that "looks" like the ancestral condition, usually the loss or reduction of some feature. The absence of a structure may be due either to the fact that the species (and its ancestors) never had it in the first place, or to its subsequent loss. It is usually difficult, if not impossible, to distinguish between these two hypotheses simply by studying the character itself. That conclusion relies on considering all the evidence on the phylogeny of the species.

How, then, can you determine if a character is ancestral or derived? First, we must divorce ourselves from the idea that in science we can actually determine the truth of any statement. Rather, we form hypotheses that are based on evidence and subject to testing. The dominant means of hypothesizing character polarity, whether it is ancestral or derived, is to look at the form in which the character occurs in groups outside of our group of interest. The species being studied constitute the in-group; those species with which the characters are being compared in order to hypothesize their polarity make up the out-group. The state in which the character is found in the out-group is hypothesized to be the plesiomorphic condition. Thus the choice of species to be included in the out-group is critical to the analysis. Ultimately, out-group analysis is based on the principle of parsimony (see later discussion).

The hierarchical pattern of distribution of synapomorphies is represented as a treelike branching diagram known as a cladogram (Figure 3-1). The two groups of species that diverge at any node are sister groups. A cladogram resembles many of the classical illustrations of the "tree of life," but with an important exception. On a cladogram, the units that are being studied—often species, but the unit could be a group of species as well—are shown only at the apex of the diagram, at the ends of the branches. If a fossil species is included, it is found at the end of a branch, just as any living species would be. The internodes, then, do not represent ancestral species. The order in which the groups are listed (for example, from top to bottom in Figure 3-1) is of no significance; the cladogram can be rotated about any of its nodes. The meaning of a clado-

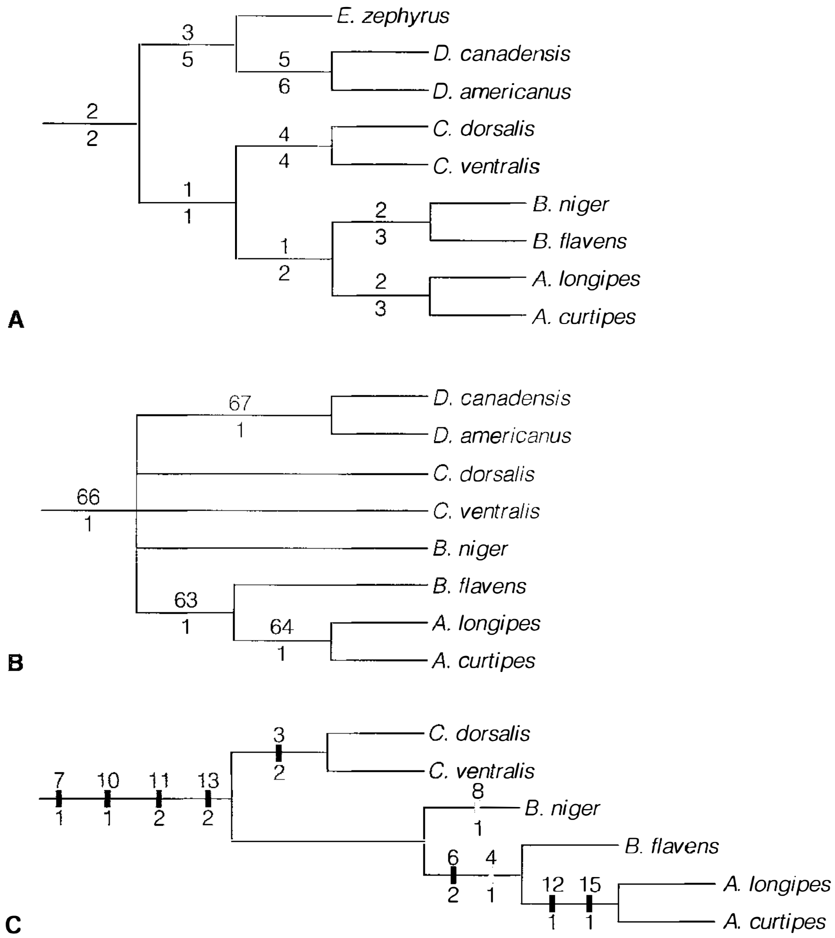

Figure 3–1 Samples of drawing conventions for depicting cladograms. A, Cladogram with a standard length used for each branch. The numbers above each branch are the number of synapomorphies defining it, the numbers below are decay indices, indicating the minimum number of additional steps in a cladogram that did not include that branch. **B**, Cladogram illustrating a polytomy (at the base), an area of the cladogram for which either no evidence is available to resolve it into a series of dichotomous branches, or for which the available data conflict. In this case the number above a branch is a bootstrap value (in %), indicating the frequency with which that branch appears when the data set is randomly resampled for characters; the number below the branch is a decay index. C, A cladogram in which the synapormophies are indicated on the branches in which they appear. The number above the branch represents the character, the number below indicates which state the character exhibits. The different format of the cross-hatch (either solid black or gray) is used here to indicate if the synapormorphy is unique or if it also occurs elsewhere in the cladogram. None of the conventions shown is standardized, and the caption should always explain such details to the reader.

gram lies in the hierarchy illustrated by the branching diagram.

Relationship, in the sense of phylogenetic systematics, is defined as the relative recency of common ancestry. In other words, given three species—A, B, and C—species A and B are more closely related if they share a more recent common ancestor with each other than either does with C. If we assume that the animal kingdom is monophyletic, that all animals share a common ancestor, then any pair of animals is related in some sense. The critical issue is not if two species are related, but how closely related they are. Thus any meaningful phylogenetic hypothesis must deal with *at least* three species.

In the simplest case of three taxa (species or groups of species), there are only three possible patterns of relationship: either A+B are most closely related, A+C, or B+C. With four terminal taxa (A to D) the number of possible patterns increases to 15, with five taxa there are 105 possible patterns; for ten taxa, over 34 million possibilities; and the number continues to grow exponentially. What criteria are used to distinguish among all these possibilities?

The most commonly used metric is the number of "steps" on each tree. Each individual step represents the change in a character from the ancestral to derived condition. These changes include the possible hypothesis that a character changes back to what appears to be the ancestral state, that is, a character reversal. One dominant method of analysis then applies the principle of parsimony to select the optimal cladogram. The cladogram that has the fewest number of steps, the shortest cladogram, is held to be the best explanation of the data at hand. All other, longer cladograms require unnecessary hypotheses of character change. The principle of parsimony (Occam's razor) holds that the best explanation for a phenomenon is the simplest one that accounts for the observed data. This should not be interpreted to mean that evolution proceeds by the most parsimonious path. We have clear evidence that that notion would be false. Rather, parsimony simply requires us to have evidence to support hypotheses of relationship. To do otherwise means that any cladogram that appealed to a researcher could be claimed to be the "best" on grounds that had nothing to do with science.

Phylogenetic analyses of sequence data often use a different optimality criterion by which to judge the best cladogram: maximum likelihood. This method relies on specifying a model of base transformation; for example, what is the probability of an adenine residue changing to a thymine at a given position? The overall likelihood of a set of cladograms is calculated, and the one with the highest likelihood is given preference. Recently, Bayesian analysis methods have begun to be developed to find the most likely phylogenetic hypothesis (cladogram) given the observed data and model of base substitution.

Often the internodes of a cladogram are labeled with information that indicates the support for the hypothesis that it represents a monophyletic group. This may be a listing of the apomorphic characters that define that section of the cladogram; also commonly found are bootstrap support values or Bremer support values. A bootstrap value represents the percentage of times that grouping (or clade) appears when a large number of subsets of the original data set are analyzed. Some researchers think a high number (say, 98%) indicates that the data strongly support the hypothesized monophyletic group. Note, however, that this is not a statistical test in the usual sense of the term. The hypothesis, the proposed monophyletic group, is not rejected on the basis of this number. A Bremer support value indicates the number of further steps that would be added to the entire cladogram if the clade under consideration were not included and its species were placed in a different pattern. The significance of the absolute value of such a number, then, depends on the total length of the cladogram, which, in turn, depends on the number of taxa and characters.

The student will often see published cladograms in which a node does not give rise to two branches but instead gives rise to three or more. This polytomy indicates either that there are no data to support any one of the possible sets of dichotomous possibilities at that point, or that the data conflict so that no one possibility is more parsimonious (or likely) than another. Polytomies are expressions of ignorance or ambiguity in the underlying data. Although it is biologically reasonable to believe that an ancestral species could give rise, more or less simultaneously, to three or more daughter species, the methodology of cladistics, and of science in general, compels us to search for a completely dichotomously branching cladogram. To do otherwise would be to actively ignore the phylogenetic signal that does exist in the data.

It is probably becoming clear at this point that calculating the most parsimonious cladogram for a group of any size requires the use of a computer and cladistic software. Only in cases with a relatively small number of species or an unambiguous data set is it possible to arrive at the best answer manually. A number of software packages are now available for these analyses; two of the most popular are PAUP (Phylogenetic Analysis Using Parsimony) and the WinClada package. MacClade is a popular tool for visualizing and manipulating data on cladograms. However, even with the most powerful hardware and software some phylogenetic problems are inherently intractable. In many cases, the analysis results in large numbers of equally parsimonious trees. In such cases, authors often resort to publication of consensus trees to depict at least the components that all the solutions have in common.

Classifications

In a formal biological classification, species are grouped into monophyletic groups. Such groups are called taxa (sing., taxon). These taxa are arranged in a hierarchical pattern. The most commonly used categories or levels in the system of zoological classification are the following (listed from most inclusive to least):

- Phylum
  - Subphylum
    - Class
      - Subclass
        - Order
          - Suborder
            - Superfamily
              - Family
                - Subfamily
                  - Tribe
                    - Genus
                      - Subgenus
                        - Species
                          - Subspecies

In this scheme, the animal kingdom is divided into a number of phyla (sing., *phylum*). Each phylum is divided into classes, classes into orders, orders into families, families into genera (sing., *genus*), and genera into species. Finer distinctions in the levels is afforded by prefixes attached to these category names, such as *superfamily* or *subgenus.* This list provided is not comprehensive, but does illustrate the normal categories that are used. The species is probably the only level that can be assessed by objective criteria. A genus is one or more species classified together in a monophyletic group; a family is one or more genera; and so on. Any scheme of classification that is developed for a group of animals will be affected by the particular characters used, the relative weight they are given, and how they are analyzed. If different people use different characters or a different "weighting" of a series of characters, they may arrive at different classifications.

A classification is derived from a phylogeny by designating monophyletic groups for each category. Of course, a dichotomous cladogram of n species will have $n-1$ monophyletic groups. For a cladogram of any size, particularly in insects where one order may have more than 100,000 species, not all these groups are formally named. The usual approach systematists take is similar to the admonition in the Hippocratic oath to do no harm, that is, to change the formal classification where necessary to preserve the criterion of monophyly, but to keep such changes to a minimum. There is, obviously, a great deal of room here for individual interpretation, and, as a result, several alternative classifications may be in use at any point in time, particularly for popular groups (such as butterflies).

Many groupings of insects first recognized by early systematists such as Fabricius and Latreille are still recognized today as valid monophyletic groups. Examples include the Apocrita (Hymenoptera), Brachycera (Diptera), Ditrysia (Lepidoptera), and Polyphaga (Coleoptera). However, in traditional classifications these taxa were often paired off in contrast with another group, Symphyta versus Apocrita, Nematocera versus Brachycera. These "sister" taxa often are not true sisters in the phylogenetic sense, because they are widely acknowledged to be paraphyletic groups. As such, according to the principles of phylogenetic systematics they should not be formally recognized. Entomologists are, indeed, moving in that direction, but it is a slow and gradual process. We have continued to include some of these groups in the classifications in each chapter, partly because the names are so widely used that it is important for the student to learn them. However, in the long run classifications are based on scientific hypotheses, and these hypotheses may be changed or rejected as understanding of insect diversity increases. Thus expect to see changes in those classifications reflecting the underlying scientific research, and embrace the changes as indications of advances in the understanding of insect diversity and relationships.

Nomenclature

Animals have two types of names, scientific and common. Scientific names are used throughout the world, and every known animal taxon has a scientific name unique to it. Common names are vernacular names, and they are often less precise than scientific names. (Some common names are used for more than one taxon, and a given animal taxon may have several.) Many animals lack common names because they are small or seldom encountered.

Scientific Nomenclature

The scientific naming of animals follows certain rules, outlined in the *International Code of Zoological Nomenclature* (ICZN 1999). Scientific names are latinized, but they may be derived from any language or from the names of people or places. Most names are derived from Latin or Greek words and usually refer to some characteristic of the animal or group named.

The names of groups above genus are latinized nouns in the nominative (subject case) plural. The names of genera and subgenera are latinized nouns in the nominative singular. Specific and subspecific names may be adjectives (descriptors, or modifiers), present or past participles (forms) of verbs (action words), or nouns (names of things or places). Adjectives and participles must agree in gender (masculine, feminine, or neuter) with the genus name, and nouns are in either the nominative or the genitive (possessive) case.

The scientific name of a species is a binomen; that is, it consists of two words: the genus name and a specific epithet. That of a subspecies is a trinomen: the genus name, the specific epithet, and a subspecific epithet. These names should be printed in *italics* (if written or typewritten, italics can be indicated by underlining). Names of species and subspecies are sometimes followed by the name of the author, the person who described the species or subspecies. Authors' names are not italicized. The appended author name is sometimes important in dealing with the systematics of a species or in cases where the same name has been proposed for two different species (a case of homonymy). In most other cases, it is simply superfluous and adds nothing more than a false sense of authority to the person citing the name. The names of genera and higher categories always begin with a capital letter; species and subspecies names never do and generally are not cited without the name or abbreviation of the genus. If the author's name is in parentheses, it means that the species (or subspecies, in the case of a subspecies name) was described in some genus other than the one in which it is now placed. For example,

Papilio glaucus Linnaeus[1]—the tiger swallowtail. The species *glaucus* was described by Linnaeus in the genus *Papilio*.

Leptinotarsa decemlineata (Say)—the Colorado potato beetle. The species *decemlineata* was described by Thomas Say in the genus *Doryphora*, and this species has since been transferred to the genus *Leptinotarsa*.

Argia fumipennis (Burmeister)—The species *fumipennis* was described by Hermann Burmeister in some genus other than *Argia* and has subsequently been transferred to the genus *Argia*. There are three subspecies of this species in the eastern United States: a northern subspecies (*violacea*) with clear wings and considerable violet coloration, a southern subspecies (*fumipennis*) with smoky wings and considerable violet coloration, and a subspecies in peninsular Florida (*atra*) with very dark wings and dark brownish (not violet) coloration. These three subspecies are listed as *Argia fumipennis violacea* (Hagen), *Argia fumipennis fumipennis* (Burmeister), and *Argia fumipennis atra* Gloyd. Hagen's name in parentheses means *violacea* was described in a genus other than *Argia*, but there is no way of knowing from this name whether *violacea* was originally described as a species, as a subspecies of *fumipennis*, or as a subspecies of some other species. Gloyd's name without parentheses means *atra* was originally described in the genus *Argia*, but there is no way of knowing from this name whether *atra* was originally described as a species of *Argia*, as a subspecies of *fumipennis*, or as a subspecies of another species of *Argia*. In fact, Hagen originally described *violacea* as a species of *Agrion*, and Gloyd originally described *atra* as a subspecies of *Argia fumipennis*.

Some entomologists have used trinomials for what they have called "varieties," for example, *A-us b-us*, var. *c-us*. Other ranks may also be found, including form, stirps, race, and so forth. Such names, if published before 1961, are assumed to be names of subspecies, in which case the "var." in the name is dropped, or if they are shown to designate an individual variant, they are considered "infrasubspecific" categories, which are not covered by the *International Code of Zoological Nomenclature*. Such names published after 1960 are considered to designate individual variants ("infrasubspecific" categories), not covered by the rules. The taxonomic categories just listed apply to populations and not to individual variants such as color forms, sexual forms, and seasonal forms.

A species referred to but not named is often designated simply by "sp." For example, "*Gomphus* sp." refers to a species of *Gomphus*. More than one species may be designated by "spp."; for example, "*Gomphus* spp." refers to two or more species of *Gomphus*.

The names of categories from tribe through superfamily have standardized endings and hence can always be recognized as referring to a particular category. These can be illustrated by some taxa of bees, as follows:

Superfamily names end in *-oidea*; for example, Apoidea: the bees. Note that the names of some genera and categories above the level of family can have the same ending.
  - *Family* names end in *-idae*; for example, Apidae: cuckoo bees, digger bees, carpenter bees, orchid bees, bumble bees, and honey bees.
    - *Subfamily* names end in *-inae*; for example, Apinae: orchid bees, bumble bees, and honey bees.
      - *Tribe* names end in *-ini*; for example, Apini, honey bees.

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[1] Throughout this book Linnaeus is abbreviated "L."

Types. Whenever a new taxon (from subspecies to superfamily) is described, the describer is supposed to designate a **type**, which serves to anchor the name to a taxonomic concept. The type of a species or subspecies is a single specimen (the type, or **holotype**); the type of a genus or subgenus is a species (the **type species**); and the type of a taxon from tribe through superfamily is a genus (the **type genus**). Names of taxa from tribe through superfamily (see the previous examples) are formed by adding the appropriate ending to the root of the name of the type genus. For the type genus *Apis* in the previous examples, the stem is *Ap-*. If a species is divided into subspecies, the particular subspecies that includes the holotype of the species has the same subspecific name as its specific name (for example, *Argia fumipennis fumipennis*). Similarly, if a genus is divided into subgenera, the subgenus that includes the type species of the genus has the same subgenus name as genus name—for example, *Formica (Formica) rufa* L. (The name in parentheses is the subgenus.) As concepts of the limits of species or other taxa are revised, it is often necessary to refer to the available types (and ultimately the holotypes of the relevant species) to determine to which concepts of taxa of the systematist the types belong, and, thus, to determine which name or names are applicable to it. The significance of holotypes has to do with nomenclature; they do not represent a "typical" member of a species.

Priority. The starting point of modern binomial zoological nomenclature was the publication of 10th edition of Linnaeus' *Systema Naturae*; the date is taken as 1 January 1758. It often happens that a particular taxon is described independently by two or more people, and hence may have more than one name. In such cases the first name used from 1758 on (if the describer has followed certain rules) is the correct name, and any other names become synonyms and should no longer be used. A particular name is often used for a long time before someone discovers that another name has priority over it.

Sometimes a person describing a new taxon gives it a name that has previously been used for another taxon; if those taxa involved are at the same taxonomic level, the names are termed *homonyms*, and all but the oldest must be discarded and the taxa renamed. There cannot be two (or more) species or subspecies with the same name in a given genus. There cannot be two (or more) genera or subgenera in the animal kingdom with the same name. Nor can there be two (or more) taxa in the family group of categories (tribe through superfamily) with the same name (although the names of the typical subdivisions will be the same except for their endings). The fundamental rule is that every animal taxon must have a unique name.

Because of the large number of animal taxa and the vast amount of zoological literature, errors in naming (homonyms and synonyms) are not easy to discover. As they are discovered, it becomes necessary to change names, not only of genera and species, but also of families and even orders. The problems of priority in scientific nomenclature are often very intricate, and it is sometimes difficult to determine just what name is the correct one. Name changes may also result from increased knowledge. This added knowledge may indicate that groups should be split or combined, resulting in name changes for some of the groups involved.

In cases where two or more names for a group have been in fairly wide use, we have listed in this book first what we believe to be the correct name and have listed other names in parentheses.

Pronunciation

The pronunciation of some of the technical names and terms used in entomology may be found in a good dictionary or glossary, but very few texts or references give the pronunciation of the bulk of scientific names. There *are* rules for the pronunciation of these names, but few entomologists are familiar with them, and many names are pronounced differently by different people and in different countries. We have therefore included some of the general rules by which technical names and terms used in zoology are generally pronounced in American English. We realize that not all entomologists will agree with the pronunciation of some names. There are two reasons for such disagreement: (1) a given pronunciation, whether it follows the rules or not, may become established through usage as the "correct" pronunciation; and (2) the correct pronunciation of many scientific names depends on the derivation of the name and the vowel sound in the source language, and it is difficult or impossible to determine the derivation of some names. Hence there will always be a question as to the correct pronunciation of some scientific names.

The principal rules for the pronunciation of scientific names and terms are outlined here:

Vowels. All vowels in scientific names are pronounced. Vowels are generally either long or short, and in the examples that follow a long vowel sound is indicated by a grave accent (ì) and a short vowel sound by an acute accent (í); for example, *màte*, *mát*, *mète*, *mét*, *bìte*, *bít*, *ròpe*, *rót*, *cùte*, *cút*, *bỳ*, *sýmmetry*. A vowel at the end of a word has the long sound, except when it is an *-a*; a final *-a* has the *uh* sound, as in *idea*. The vowel in the final syllable of a word has the short sound, except *-es*, which is pronounced *ease*.

Diphthongs. A diphthong consists of two vowels written together and pronounced as a single vowel. The diphthongs are *ae* (pronounced è, rarely é), *oe* (usually pronounced è, rarely é), *oi* (pronounced as in *oil*), *eu* (pronounced *ù*), *ei* (pronounced *ì*), *ai* (pronounced *à*), and *au* (pronounced as in *August*). The final *-ae* in family and subfamily names is generally pronounced *è*. The combination *ii* is pronounced as two syllables and is therefore not a diphthong.

Consonants. *Ch* has the *k* sound, except in words derived from a language other than Greek. When *c* is followed by *ae*, *e*, *oe*, *i*, or *y*, it has the soft (*s*) sound; when it is followed by *a*, *o*, *oi*, or *u*, it has the hard (*k*) sound. When g is followed by *ae*, *e*, *i*, *oe*, or *y*, it has the soft (*j*) sound; when it is followed by *a*, *o*, *oi*, or *u*, it has the hard sound (as in *go*). In words beginning with *ps*, *pt*, *ct*, *cn*, *gn*, or *mn*, the initial letter is not pronounced, but when these letters appear together in the middle of a word, the first letter is pronounced (for example, the *p* is not pronounced in the word *pteromorph*, but it is pronounced in the word *Orthoptera*). An *x* at the beginning of a word is pronounced as *z*, but as *ks* when it appears elsewhere in a word. When a double *c* is followed by *e*, *i*, or *y*, it is pronounced as *ks*.

Accent. The accented syllable is either the penult or the antepenult (very long words may have a secondary accent on a syllable near the beginning of the word). The principal rules governing the syllable accented and the vowel sound (whether long or short) are as follows:

1. The accent is on the penultimate syllable in the following cases:
    a. When the name contains only two syllables; for example, *Àpis*, *Bómbus*.
    b. When the penult contains a diphthong; for example, *Culicòides*, *Hermileùca*, *Lygaèus*.
    c. When the vowel in the penult is followed by *x* or *z*; for example, *Coríxa*, *Prodóxus*, *Agromỳza*, *Triòza*.
    d. When the vowel of the penult is long. Whether the penult vowel is long or short often depends on the derivation of the word and the vowel sound in the source language. The vowel *e* in a word derived from the Greek is long if the vowel in the Greek word is eta (η), but short if it is epsilon (ϵ); for example, in words derived from the Greek μηροσ, meaning *thigh*, the *e* is long (*Diapheromèra*, *epimèron*), whereas in those derived from the Greek μϵροσ, meaning *part*, the *e* is short (Heterómera). Similarly, the vowel *o* in a word derived from the Greek is long if the vowel in the Greek word is omega (ω), but short if it is omicron (o); for example, in words derived from the Greek σωμα meaning *body*, the *o* is long (*Calosòma*, *Malacosòma*), whereas in those derived from the Greek στομα, meaning *mouth*, it is short (*Melanóstoma*, *Belóstoma*, *epístoma*). The penult vowel is long in subfamily names (for example, *Sphecìnae*) and tribe names (for example, *Sphecìni*); in tribe names, the final *i* is also long.
2. In other cases the antepenult is accented.

Common Names of Insects

Because there are so many species of insects, and because so many of them are very small or poorly known, relatively few have common names. Those that do are generally particularly showy insects or insects of economic importance. American entomologists recognize as "official" the common names in a list published every few years by the Entomological Society of America, but this list does not include all species of insects (and other arthropods) to which common names have been applied. The common names used in this book for individual species have been taken from this list or have been obtained from other sources.

Many common names of insects refer to groups such as subfamilies, families, suborders, or orders, rather than to individual species. The name *bark beetle*, for example, refers to all species in the subfamily Scolytinae of the family Curculionidae. The name *leaf beetle* applies generally to all species in the family Chrysomelidae. The name *beetle* applies to all species in the order Coleoptera. The name *damselfly* applies to the entire suborder Zygoptera, of which there are hundreds of species.

Most common names of insects that consist of a single word refer to entire orders (for example, *beetle*, *bug*, *caddis*, *cockroach*, and *termite*). Some (such as *bee*, *damselfly*, *grasshopper*, and *lacewing*) refer to suborders or groups of families. Only a few (such as *ants*) refer to families. Most common names applying to families consist of two or more words, the last being the name of the larger group, and the others descriptive (for example, *brown lacewings*, *click beetle*, *soldier flies*, and *small winter stoneflies*).

The members of a group are often referred to by an anglicized form of the group name. For example, insects in the order Hymenoptera may be called *hymenopterans;* the wasps in the superfamily Chalcidoidea are called *chalcidoids;* those in the Sphecidae are called *sphecids;* and those in the subfamily Nyssoninae may be called *nyssonines*. It is a common practice to use such a form of the family or subfamily name as a common name.

The names "fly" and "bug" are used for insects in more than one order, and the way the names of these insects are written may indicate the order to which the insect belongs. For example, when a fly belongs to the order Diptera, the "fly" of the name is written in this book as a separate word (for example, *black fly*, *horse fly*, and *blow fly*); when it belongs to another order, the "fly" of the name is written together with the descriptive word (for example, *dragonfly*, *butterfly*, and *sawfly*). When a bug belongs to the order Hemiptera, the "bug" of the name is written as a separate word (for example, *damsel bug, stink bug,* and *lace bug*); when it belongs to another order, the "bug" of the name is written together with the descriptive word (for example, *mealybug, ladybug, junebug,* and *sowbug*). Unfortunately, this practice is not universally accepted.

The Identification of Insects

When someone encounters an insect, one of the first questions asked is "What kind of insect is it?" (Or perhaps that is the second question after "Will it bite me?") One of the principal aims of the beginning student in any field of biology is to become able to identify the organisms he or she is studying. The identification of insects differs from the identification of other types of organisms only in that it is likely to be somewhat more difficult, because there are more kinds of insects than anything else.

Four things complicate the problem of insect identification. First, there are so many different species of insects that the beginner may be discouraged about ever becoming proficient in insect identification. Second, most insects are small, and the identifying characters are often difficult to see. Third, many insects are poorly known, and when they are finally identified, you may have only a technical name (which you may not understand) and little biological information. Fourth, many insects go through very different stages in their life history, and you may come to know insects in one stage of their life cycle and still know very little about those same insects in another stage.

There are about five ways in which a student may identify an unknown insect: (1) by having it identified by an expert, (2) by comparing it with labeled specimens in a collection, (3) by comparing it with pictures, (4) by comparing it with descriptions, (5) by using an analytical key, or by a combination of two or more of these procedures. Of these, obviously the first is the simplest, but this method is not always available. Similarly, the second method may not always be available. In addition, the use of a collection is of limited value if you do not know the characteristics that distinguish the species in a particular group. In the absence of an expert or a labeled collection, the next best method is usually to use a key. In the case of particularly striking or well-known insects, the identification can often be made by the third method mentioned, but in many groups this method is unsatisfactory. No book can illustrate all kinds of insects and still sell for a price a student can afford to pay. Where an unknown insect cannot be definitely identified by means of illustrations, the best procedure is to use an analytical key and then to check the identification by as many of the other methods mentioned as possible. Identification from pictures is often unsafe, because in many instances one type of insect looks a great deal like another.

As a general rule, in this book identification is carried only to family. To go much further usually requires specialized knowledge and is beyond the scope of this book. Identifying insects only to family reduces the number of names from many thousand to several hundred, and of these probably only 200 or fewer are likely to be encountered by the average student. We reduce the problem still further by being concerned largely with adults. Thus insect identification becomes less formidable.

The Keys in This Book

Analytical keys are devices used to identify all sorts of things, living as well as nonliving. Different keys may be arranged somewhat differently, but all involve the same general principles. You run an insect (or other organism) through a key in steps. At each step you face two (rarely more) alternatives, one of which should apply to the specimen at hand. In our keys either a number or a name follows the alternative that best fits the specimen. If there is a number, the next step is the couplet with this number. Thus each step leads to another step and its alternatives until a name is reached.

The couplets of alternatives in our keys are numbered 1 and 1′, 2 and 2′, and so on. In the first half of each couplet after the first is a number in parentheses. This is the number of the couplet from which that couplet is reached, and it enables the student to work backward in the key if a mistake is discovered. This method of numbering also serves as a check on the accuracy of the organization of the key. In a few large keys, certain couplets may be reached from more than one previous couplet, and this fact is indicated by two or more numbers in parentheses.

The keys in this book have been prepared from three principal sources: other published keys, descriptions, and an examination of specimens of the groups concerned. Many are taken largely from previously published keys (generally with some changes in wording or organization), but some represent a new approach. Our aim with each key has been to prepare something that is workable for practically every species (or specimen) in the groups covered. Most of these keys have been tested by student use over a number of years. In many of the insect orders (particularly the larger ones), some groups key out in more than one place. This is the case in two types of situations: (1) where there is significant variation within the group, and (2) with borderline cases where the specimen seems to fit both alternatives of a couplet. In the latter situation, a specimen should key out correctly from either alternative. Although our intent is that these keys will work for every specimen, we realize that species or specimens in many groups are erratic in their characters. We have sought to include as many as possible of these atypical forms in our keys, but a few may not key out correctly. We believe our keys should work for 95% or more of the insects of the continental United States and Canada. We believe the user of our keys is more likely to reach an impasse because of an inability to see or interpret a character than because of a discrepancy in the key.

When a determination is reached in the key, check the specimen against any illustrations or descriptions available. If these do not fit the specimen, then either a mistake has been made somewhere or the specimen is one that will not work out correctly in the key. In the latter event, save the specimen until you can show it to an expert. It may be something rare or unusual.

Success in running an insect through a key depends largely on understanding the characters used. In many cases in this book, the key characters are illustrated. Often several characters are given in each alternative. In case one character cannot be seen or interpreted, use the other characters. If at any point in the key you cannot decide which way to go, try following up both alternatives and then check further with illustrations and descriptions when you reach a name.

A great many families of insects are very unlikely to be encountered by the general collector because they contain small or minute forms that may be overlooked, because they are quite rare, or because they have a very restricted geographic range. Such families are indicated in most of our keys by an asterisk, and couplets containing such groups can often be skipped by the beginning student.

Measurements in this book are given in metric units. Tables for converting these to English units follow the table of contents.

Analytical keys are made for people who do not know the identity of a specimen they have. Once a specimen has been identified with a key, subsequent identifications of this same insect may often be based on such characters as general appearance, size, shape, and color, without reference to minute characters.

It will be apparent very early during your work in identifying insects that you need a good binocular microscope to see many characters of the insect. Most insects, once you know what to look for, can be identified with a good hand lens (magnification about 10×).

The mere identification and naming of insects should not be the student's final objective in insect study. There is much more of interest in insects than just identifying them. Go further, and learn something of the habits, distribution, and importance of insects.

Geographic Coverage of This Book

The taxonomic treatment in this book of the various insect orders and the other groups of arthropods applies to the fauna of North America north of Mexico. A few insects in other parts of the world are mentioned, but the characters given for each group (and the keys) apply to North American species and may not apply to all other species occurring outside of North America. The terms North America and North American refer to that portion of the continent north of Mexico. Where the geographic range of a group in North America is more or less limited, information on this range is given. Groups for which there is no information on range are widely distributed in North America.

References

Borror, D. J. 1960. Dictionary of Word Roots and Combining Forms. Palo Alto, CA: Mayfield, 134 pp.

Brown, R. W. 1978. Composition of Scientific Words. Washington, DC: Smithsonian Institution Press, 882 pp.

Crowson, R. A. 1970. Classification and Biology. New York: Atherton Press, 350 pp.

Eldredge, N., and J. Cracraft. 1980. Phylogenetic Patterns and the Evolutionary Process: Method and Theory in Comparative Biology. New York: Columbia University Press, 349 pp.

Hennig, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Berlin: Deutscher Zentralverlag.

Hennig, W. 1965. Phylogenetic systematics. Annu. Rev. Entomol. 10:97–116.

Hennig, W. 1966. Phylogenetic Systematics. Urbana: University of Illinois Press, 263 pp.

International Commission on Zoological Nomenclature. 2000. International Code of Zoological Nomenclature, 4th ed. London: The International Trust for Zoological Nomenclature 1999, 306 pp.

Mayr, E., and P. D. Ashlock. 1991. Principles of Systematic Zoology, 2nd ed. New York: McGraw-Hill, 475 pp.

Schuh, R. T. 2000. Biological Systematics: Principles and Applications. Ithaca, NY: Comstock Publishing Associates, Cornell University Press, 236 pp.

Stoetzel, M. B. 1989. Common Names of Insects & Related Organisms 1989. College Park, MD: Entomological Society of America, 199 pp.

Wiley, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. New York: Wiley, 439 pp.

Winston, J. E. 1999. Describing Species: Practical Taxonomic Procedure for Biologists. New York: Columbia University Press, 518 pp.

4

Behavior and Ecology[1]

The importance of insects is determined largely by what they do. The accounts of various insect groups in this book say a good deal about their behaviors and natural histories. In this chapter we discuss and illustrate general principles of insect behavior and ecology and draw together the kinds of activities common to insects in general.

Properties of Behavior

A common misconception is that compared to vertebrates, insects have simple and limited behavioral repertoires, because insects are constrained by small nervous systems and short lives. Yet, like other animals, insects are not predictable automatons. They do not remain inert until provoked by particular stimuli to perform specific acts, and when stimulated to respond in a characteristic way, they are not limited to a rigid preprogrammed set of movements. Instead, much of insect behavior is outwardly spontaneous and can adjust to particular circumstances. The jobs insects carry out during their lives are the result of a complex interplay between environmental stimuli, internal state, and experience, and the way their activities are organized often is exceedingly complex.

Composition and Pattern

The basic unit of insect behavior is the reflex: One kind of receptor, when stimulated, causes a specific group of muscles to contract, outwardly visible as a body movement. Yet even the simplest behaviors following this stimulus–response rule engage large suites of reflexes, involving dozens or hundreds of sensory receptors and muscle sets. These combined reflexes result in a coordinated group of movements that perform some useful element of behavior. An example is food chewing, which consists of coordinated movements among mandibles, maxillae, hypopharynx, and other structures that handle and shred food after it is bitten off but before it is swallowed. The stimulus that triggers a particular complex of movements is often called a *releaser*. The resulting behavior, once initiated, is exactly the same each time it is performed; that is, it is stereotypic and is called a *fixed-action pattern*. Most motor patterns, however, vary according to stimulus input, both when they are initiated and while they are being performed. Thus, even though the end result is the same, the insect's behavior is adjusted to meet the precise circumstances of the situation. These *modal-action patterns* are less stereotypic, because they constantly adapt to changes in body position relative to external objects. Thus insects walk or fly according to a very specific sequence of leg or wing movements, operated by a *central pattern generator*, but they continuously make fine adjustments in these movements to stay on course over rough terrain or in air turbulence. Even nest building, which is a complicated process and may be interrupted by the need to gather more nest material or to feed or rest, is a modal-action pattern in the broad sense. Piece by piece, the insect adds nest material where it is needed most, adjusts for damage, and works around natural obstacles. However, the insect adds material to the nest in a species-specific way, and completed nests of a species are nearly identical.

Orientation is the ability of an insect to be guided by local external circumstances. Technically, it is the modification of body position or movement with re-

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[1] This chapter was contributed by Woodbridge A. Foster.

spect to some variation in the distribution of environmental stimuli. Even behavior patterns that start spontaneously, such as the search for food or a mate, nevertheless typically are guided by the arrangement of various visual, chemical, or mechanical stimuli. Insects' oriented movements are categorized as either *kineses* or *taxes*. *Kineses* are simply changes in the speed of locomotion or rate of turning as an insect moves and encounters an increased or decreased stimulus intensity, without regard to the direction, source, or gradient of the stimulus. Kineses have the effect, through random movements, of bringing the insect into a favorable zone or away from an unfavorable one. For example, an insect exhibiting positive klinokinesis with respect to temperature makes more turns as it encounters increasingly favorable temperatures, so it tends to remain in zones of optimal temperature. *Taxes*, in contrast, are positions and movements with respect to the source, direction, or gradient of a stimulus (for example, chemotaxis, phototaxis). Different mechanisms may be involved. Insects can move up or down a stimulus gradient (toward or away from its source) by balancing the stimuli on the right and left, either by turning alternately right and left or by sampling both sides simultaneously (*klinotaxis* and *tropotaxis*, respectively), or by maintaining a "fix" on the source itself (*telotaxis*). They also can use telotaxis to maintain themselves at a fixed angle from the stimulus source (*menotaxis*). This allows them to remain right side up with respect to skylight or gravity and to walk or fly in a straight line through varied landscape, using the sun or moon as a fixed frame of reference—essentially as a compass. These basic kinds of orientation mechanisms, applied to problems such as nest building in a difficult spot, allow an insect to behave effectively in a complex and changing world, even when the guided behavior is entirely independent of experience.

When insects locate food and mates through vision, sound, or chemicals, accurate orientation is essential. They typically use tropotaxis or telotaxis to orient toward attractive sounds and visual objects at a distance. At close range they follow gradients of a chemical, temperature, or humidity by employing klinotaxis or tropotaxis. However, the need for flying insects to locate a distant source of volatile chemicals presents a special problem. It is impossible for them to get a fix on the source by scanning the environment, and stimulus gradients are lost beyond a few centimeters from the source, as chemicals waft downwind in dilute, meandering swirls and filaments. Instead, they orient upwind (positive *anemotaxis*) in the presence of pulses of the stimulating odor, guided in their forward progress by the passage of objects on the ground beneath them. This behavior has the effect of bringing them very close to the odor's source. If the odor stimulus is lost, the insect ceases to fly upwind and makes erratic turns or reverts to a crosswind or downwind searching flight. In moths, males progressing upwind in the presence of female sex pheromone automatically zigzag across the odor plume continuously, making it more difficult to lose the scent altogether.

Some kinds of orientation remain enigmatic. The migration of monarch butterflies is noteworthy because they travel thousands of kilometers between the northern reaches of their distribution and very localized southern overwintering sites. The slow northward migration involves up to three successive generations of butterflies. Thus all adults that overwintered are dead by the time the population reaches its northern limit during the summer, and those that fly back to the overwintering site in the south have never been there before. Research evidence indicates that they use a time-compensated sun compass, and perhaps also geomagnetic cues, to guide them toward the correct longitude and latitude. If this is correct, it suggests that the monarch butterflies have an innate sense of what those coordinates should be, which vary considerably between eastern and western populations.

Behavior Modification

All behavioral abilities of an insect are inherited, but they are not invariably expressed, even under identical environmental conditions. Insects respond to certain stimuli or perform particular behaviors only when internal organs, hemolymph chemistry, and the nervous system itself are in particular states. The state of responsiveness, or motivational state, regulates the expression of even the most rudimentary and stereotypic instincts. Even learning, the ability of an insect to modify its behavior adaptively, following experience with particular external stimuli and their consequences, is an innate capacity.

Motivation: A variety of internal factors influence an insect's motivational state.

Rhythms: Nearly all insects go through cycles of activity and inactivity, the most common type being the 24-hour diel (daily) cycle. During its active phase, the insect may become active spontaneously and conduct searches for one or more necessities: mates, food, oviposition sites, or shelter. Also, at this time it is responsive to particular stimuli that it ignores when inactive. These diel rhythms are maintained by an internal clock, which is repeatedly set by the periods of dark and light. When an insect is artificially deprived of the natural time-setting light–dark transitions at regular intervals, the rhythm continues but drifts away from the 24-hour period, giving rise to the term *circadian rhythm* (around a day).

Inhibitory Feedback: An insect's state of responsiveness changes when particular behaviors cause a temporary physiological change. After eating food, an insect's threshold of response to food stimuli rises, so that it requires stronger stimuli before it will taste or ingest more. If it has ingested enough, it will not respond to stimuli of any strength. A classic example is the tarsolabellar reflex of the blow fly. When its crop is empty, if it tastes sugar with its front tarsi the fly extends its proboscis. When the crop contains a substantial sugar meal, nerves from foregut stretch receptors block the reflex. The time it takes for the fly to become motivated again (that is, has a lower threshold of the tarsolabellar reflex) is simply a function of crop volume and the rate at which the crop empties, which in turn depends on how fast absorbed sugar is depleted from the hemolymph. Some changes are the result of cyclic internal processes. For example, female insects do not exhibit oviposition behaviors until they have a batch of eggs ready to be laid.

Long-Term Physiological Changes: Other behavioral changes are long-lasting or permanent. These often are the result of development and maturation. After the final molt, adult insects do not immediately express sexual or other reproductive behaviors, but hormone-induced nervous or other internal changes lead to their expression and may last a lifetime. Juvenile hormone—a misnomer in these cases—often is the mediator. For example, juvenile hormone causes adult female mosquitoes to become sexually receptive, and after mating and insemination they immediately become unreceptive to further sexual advances by males. First mechanical stimuli from copulation and insemination, then chemical stimuli from the male's semen, abolish her receptivity for a long period or a lifetime. The tendency to migrate or to enter diapause (discussed later in this chapter) may occur only early in adult life, only when the insect is crowded during development, or only when photoperiod shortens and temperatures begin to drop. Complete metamorphosis is an extreme example of developmentally altered behavior. Larval and adult forms of the same individual are often so different, both morphologically and ecologically, that they act like different species with entirely different behavioral repertoires.

Learning: Insect learning generally is the experience-induced modification of instinctive behavior patterns, rather than formation of new behavior patterns. Learning differs from instinct mainly in that it involves properties of the nervous system that permit useful modifications in behavior, but the distinctions among motivational change, sensory adaptation, and true learning are not always obvious. Even in clear cases of learning, there exists a continuous range between preprogrammed and modified behaviors, so four categories of behavior are useful (based on Alcock 1979): (1) *closed instincts,* the fixed programs, such as courtship sequences; (2) *open instincts,* in which feedback from experience alters the program, such as improved nectar-collecting efficiency or ignoring sudden movements (habituation); (3) *restricted learning,* in which limited stimuli alter behavior in a precise way, such as attaching new meanings to stimuli (classical conditioning); and (4) *flexible learning,* in which an experience can lead to a wide range of changes in the behavior pattern, such as familiarity with unique landscapes (exploration or latent learning) and reinforcement of modified behavior (operant conditioning). The ability to achieve any of these acts, and the constraints placed on them, have a genetic basis. Modification by learning is most valuable to species that live where information is reliable for extended periods within the lifetime of the insect, but not reliable over many generations or over the population's entire range. Information that remains reliable need not be learned and can be committed to rigid stimulus–response programming. Thus, with instinct, short-lived insects get it right the first time.

Insects are capable of most types of learning known to animals. The first three, here, are well established: (1) *Habituation* is a diminished response to a stimulus after repeated exposures with no relevant consequences or associations. An example from nature is the ability of male wasps to learn to avoid being tricked into "mating" with orchid flowers that crudely mimic female wasps in appearance and odor. In captivity, insects usually habituate to startling noises, movements, and handling. (2) *Associative learning* takes two major forms: (a) In *classical conditioning,* a previously neutral stimulus, when paired with a favorable or unfavorable stimulus that normally causes a specific response, becomes a conditioned stimulus, eliciting the response by itself (the new stimulus becomes associated with the old stimulus because of its effect). For example, a honey bee, instinctively attracted to a blue flower that has a neutral odor, obtains nectar and subsequently is attracted to that odor when the blue color is absent. A variation of this is *preimaginal conditioning,* in which a neutral stimulus that an immature insect encounters while feeding on a suitable food, such as an unusual host plant, becomes the stimulus that, after metamorphosis, the adult female chooses for oviposition. This is similar to imprinting, well known in birds that become attached to the appearance of their parents, but imprinting has a narrow sensitive period soon after hatching and occurs without an associated favorable or unfavorable stimulus. (b) *Operant conditioning* is a particular act, followed by a positive or negative consequence that reinforces either performing or the refraining from that act (the act becomes associated with its consequence); a particular variant of this is sometimes known as "trial-and-error learning." For example, ants can learn how to make the appropriate left and right turns in a maze, without the help of a trail pheromone, if the reward is to reach their nest at the end of the maze. (3) In *latent learning,* an insect becomes familiar with the relationships among various neutral stimuli, even though these stimuli have no immediate positive or negative consequences. It is also called *exploratory learning.* A classic example is the ability of digger wasps to memorize the configuration of landmarks around their hidden nests so they can find them much later (Figure 4–1). (4) In *insight learning,* the animal combines information from several learning experiences and applies it to a situation never before encountered. Whether insects are capable of this very advanced form of learning is controversial. They are clearly capable of computations based on a multitude of sense data, so there is no a priori reason why they cannot process learned information from several sources and use it to meet new circumstances. The best evidence for cognition of this sort comes from tests of the ability of honey bees to form mental maps. Some experiments indicate that bees can figure out the most direct route home or to a feeding station, from places they have never been before. This requires that a bee learn the position of distant landmarks relative to one another and then interpolate the correct direction to its destination when it views the landmarks from a unique perspective.

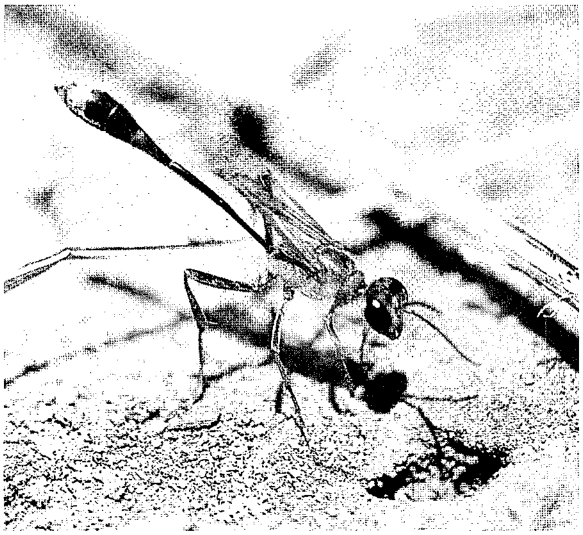

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Figure 4–1 Female digger wasp *Ammophila* (Sphecidae) at the entrance to its underground nest. Initially, she becomes familiar with its position while digging. When about to leave, she hides the nest by filling the opening with sand grains evenly with the ground's surface. As she flies away, she updates her memory of its position relative to surrounding landmarks, so that she can find it when she returns.

Temporal Structure of Behavior

Insects and other animals generally can do only one thing at a time, and their various behaviors are not performed in some haphazard sequence, although often there is an element of randomness in the probabilistic ordering of different activities. Instead, they are guided by sets of rules that are assumed to maximize reproductive success over the long run. From a study of these rules, a basic principle emerges: Different behaviors compete with one another and are mutually inhibitory, and at any given time one of them is dominant. Dominant or subordinate status is a property of the behavior's *causal system*, which is based on two things: the insect's internal causal state (or motivational state) and its external stimulus situation. Thus, whatever an insect "decides" to do (with no implication that learning-based cognition is involved) reflects the dominant status of one of the causal systems. A change in behavior may occur in four instances: (1) In *competition,* a formerly inactive behavior system becomes active because of either internal changes or changes in external stimuli, causing a rise in its dominance status, that is, increased tendency to perform or lowered threshold for expression. (2) In *chaining,* performance of the dominant behavior causes feedback that reduces its status, allowing dominance and expression of a behavior previously subdominant and therefore inhibited. Fixed chains are deterministic, and at the finest level they may be caused by (a) *sequential releasers* (as in the case of appetitive sequences, see later discussion in this chapter), in which each behavior leads to an encounter with the next releaser; (b) *interlocking releasers,* in which each behavior causes the next releaser (for example, the queen butterfly courtship, in which male and female interact in a chain of alternating behaviors); and (c) *inflexibly linked sequences,* in which one behavior follows inexorably after another, regardless of feedback (for example, the series of elements in some male courtship displays). The alternative to fixed chains are Markov chains, in which individual behaviors follow one another in a probabilistic manner, according to what behaviors preceded it and how long ago each one occurred, a pattern that occurs often in insect grooming movements. (3) In *antagonistic induction,* an insect prevented by circumstances from performing a behavior is more likely to perform it when the opportunity occurs. For example, aphids that are prevented from flying because of wind will fly sooner than aphids not exposed to wind. (4) In *temporary switching*, insects express competing behaviors randomly or according to a time-sharing method that operates independently of dominance.

Conceptual models have been developed to help people understand the organization of these underlying rules. The simplest one with broad application to insects was developed by European ethologists in the mid-1900s and assumes that behavioral control is strictly hierarchical. At the top of the hierarchy are the most basic alternative causal systems (or "centers"), such as reproduction, feeding, and migration. Within each basic system are levels of competing subsystems and sub-subsystems, each subordinate to the level above it, sharing common causal factors and a common goal but controlling finer elements of the behavior. For example, in the reproductive mode an insect may perform mating, nesting, oviposition, or food gathering for offspring, but only one task at a time. A male in the mating mode may engage in territoriality or mate pursuit, but not both simultaneously. The mate-pursuit system controls behaviors that lead progressively toward the final sequence: courtship, mate acceptance, mounting, copulation, and insemination. At each level the competing behaviors are under the control of a particular system. The insect's readiness, tendency, or responsiveness (states giving rise to the unfortunate concept of "drive") for each behavior is an outcome of internal and external stimuli and central excitatory state. According to this hierarchical hypothesis, the expression of the behavior controlled by each system at each level is blocked until its postulated *innate release mechanism* receives a particular stimulus, its releaser, which often is a simple "sign stimulus" or "token stimulus." Between successive steps in this hierarchy, *appetitive behavior* is expressed, in which oriented movements bring the insect to the next releaser. When the goal has been reached and the very stereotypic *consummatory act* is performed, feedback to the system reduces its motivational status, relative to other behavior subcategories, and one of those others becomes dominant.

Hierarchical models have been greatly expanded, and therefore complicated, to account for feedback loops and the probabilistic nature of behavioral expression. However, as models become progressively more comprehensive, they lose their heuristic value, and hypotheses about particular insects become difficult to formulate. Alternatives to hierarchical models have been used chiefly to test and explain one specific maneuver, sequence, or choice between two alternatives, rather than to offer guidelines for understanding the organization of an insect's entire behavioral repertoire. One of these approaches is *control system models* (cybernetic models), which borrow heavily from engineering and use flow diagrams, electrical schematics, and computer-like notations. These more closely represent nervous systems, are more flexible (they can easily depict both hierarchical and weblike arrangements of behaviors), and minimize the number of assumptions required. They are formed from basic conceptual patterns of control, such as chains, meshes, and positive and negative feedback loops. For example, they have been used to explain the mechanism by which a praying mantis can strike with its fore legs in the correct direction toward prey, even though its head moves independently of its thorax and can be held at different angles. A broader approach employs *optimality theory*, the general evolutionary assumption that animals evaluate their causal-state variables and tend to make decisions that minimize costs and maximize gain according to some criterion. This type of modeling can incorporate probabilistic rules and take a variety of mathematical forms. The *dynamic stochastic modeling* method, widely used in behavioral ecology, relies heavily on computer analysis to predict sequences of decisions.

The simple ethological model can account for many aspects of an insect's behavioral organization, such as spontaneous behavior, the shifting dominance of different behaviors, and sequences that lead to a goal. A famous example of an appetitive sequence is predation by the bee-wolf *Philanthus*, a digger wasp that specializes in catching honey bees to provision its nests. It starts when the wasp flies from flower to flower, searching for a bee. When it sees a moving object, the visual stimulus releases the behavior of hovering downwind of the object. If bee odor is perceived, that releases seizing the bee. And if tactile stimuli (either mechanical or chemical) are beelike, then stinging behavior is released. Thus the goal is achieved through a series of behaviors, each of which prepares the insect for encounter with the next releaser. A similar series is performed by beetles locating host plants for oviposition, mosquitoes locating vertebrate animals for blood feeding, and male moths locating pheromone-releasing females in order to mate. In the *Philanthus* case, researchers can assume that stinging the prey is the consummatory act, which lowers the motivation to collect prey, so one of the competing behaviors connected with reproduction now becomes dominant, probably oviposition, a sequence involving taking the prey to a nest and laying an egg on it. This process also has been studied in detail. A case made famous by J. Henri Fabre is *Sphex*, a wasp that digs a nest in the ground, then finds and stings a grasshopper and brings it to the nest entrance. The wasp uncovers the entrance, makes an inspection visit of the tunnel that terminates in a chamber, then returns to the surface. She grasps the prey by its antennae, pulls it down into the chamber, lays an egg on it, then exits the tunnel, covers the entrance, and leaves. Aside from raising the question of whether prey capture and nest provisioning is one or two appetitive sequences, the *Sphex* study is revealing because it tested some of the limits of flexibility in the sequence. If the prey is moved a few centimeters away from the nest entrance while the wasp is making her inspection visit, when she comes to the surface she drags the prey back to the entrance and makes another inspection visit. She will do this repeatedly, indicating a tight link between bringing the prey and conducting an inspection. Lack of feedback from the previous inspection makes her incapable of improvising in this rare circumstance.

The complexity of the entire repertoire of nesting behavior and its hierarchical organization is epitomized in some digger wasp species (Figure 4–2). *Ammophila adriaansei* females can maintain several nests at the same time, in various stages of founding and progressive provisioning with caterpillars. Experiments have demonstrated that, for each nest serviced, there are three levels of subsystems within the reproductive

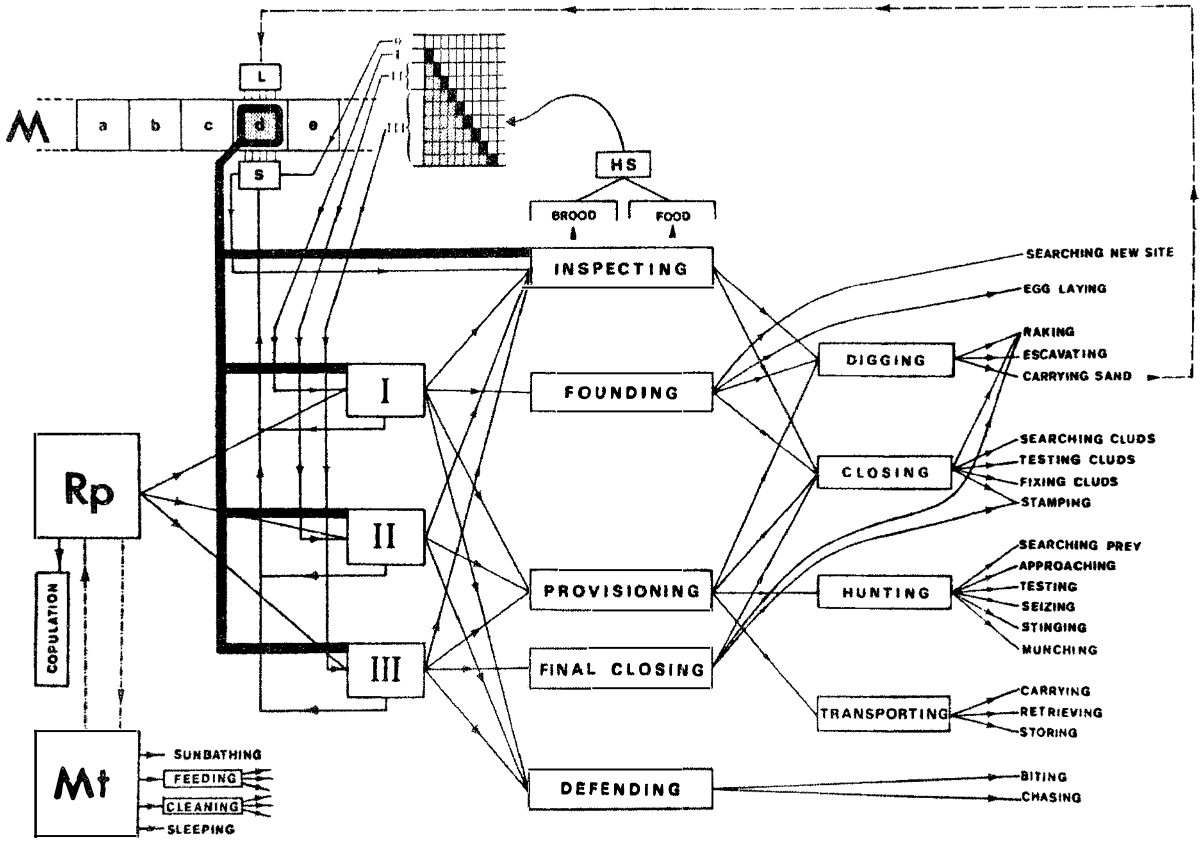


Figure 4–2 Hierarchical control of nest provisioning in the digger wasp *Ammophila adriaansei* (Sphecidae). Nesting behavior is part of the reproductive behavioral system (*Rp*), which competes with the maintenance system (*Mt*). Several nests (*a*, *b*, *c*, *d*, *e*) are in memory (*M*) at one time, but during a phase of activity on a nest, attention is not diverted to other nests. Phases I, II, and III are characterized by the amount of food (caterpillars) required, and they utilize different combinations of subsystems and sub-subsystems. Founding occurs only in Phase I and Final Closing only in Phase III. Each phase begins with Inspecting. An evaluation of the presence of a larva, its size, and the amount of food remaining determines, by heterogeneous summation (*HS*), which of the three phases will occur. If no larva is present, or if a phase is completed, the wasp scans (*S*) its memory and redirects attention to the oldest uncompleted nest. If none needs further provisioning at the time, a new one is founded and its position learned (*L*) during digging.

"system." The first level consists of three phases, each with its own motivational state and each beginning with an inspection visit prior to foraging for one or more larvae: Phase 1, one caterpillar stored, followed by oviposition; Phase 2, one to two more caterpillars provided to young larva; Phase 3, five to seven caterpillars added and nest closed for final time. Within each phase are four subsystems (founding, provisioning, final closing, and defending), founding occurring only in Phase 1, final closing only in Phase 3. And the four subsystems, plus inspecting, are expressed in one or more still finer subsystems: digging, closing, hunting, and transporting. Each of these consists of two to six distinct behaviors, such as the appetitive sequence of events involved in hunting just described. During the inspection visit, the status of the larva or remaining prey determines the total amount of provisioning that will be done before the next phase commences. In between two phases for one nest, a phase is performed for one or even two other nests. Particularly remarkable is the conclusion that the motivational state of each system persists independently for each of several nests being cared for simultaneously, each with its own memorized location. Furthermore, the wasp juggles these reproductive activities with competing maintenance activities, such as feeding, grooming, sun basking, and sleeping.

Life History Strategies

Time and Energy Budgets: The lives of insects, at the broadest level, are organized to produce the greatest number of successful, mature offspring. This number defines an insect's fitness. There are many ways to maximize fitness, but they all involve economizing time and energy, the common currencies of life. Time and energy budgets are shaped, evolutionarily, according to the principles of stringency and allocation. This means that the budgets are geared to fit the worst conditions an insect might encounter and that time and energy are allocated among survival and reproductive activities so as to maximize fitness. Each sex of an insect species typically allocates a certain portion of its time carrying out several necessary activities, such as feeding, nest making, mating, grooming, and quiescence. Quiescence serves to avoid natural enemies, inimical weather, or stressful times of day, while important internal activities continue, such as food digestion. The energy obtained by feeding is likewise budgeted among several activities that compete for energy use, such as metabolic activity, formation of sperm or eggs, locomotion, and behaviors for obtaining specific nutrients, finding mates, and defense. The best budgets are those that lead to the largest numbers of offspring and become propagated through natural selection. Thus we assume that the way insects organize and distribute their behaviors is roughly optimized for a particular insect niche. Using this kind of thinking, we can divide insects into the time minimizers, which are favored by spending the least time gathering food but the most time defending it (for example, territorial ants or burying beetles), and the energy maximizers, which gain an advantage by spending most of the time available gathering food until it is nearly gone, then dispersing to find more (for example, blow flies that develop in carcasses). These extremes in a continuum of time budget strategies fit various modes of insect life in different kinds of environments. In some ways they correspond to the oversimplified life history dichotomy based on reproductive strategies: r-strategists produce huge numbers of cheaply made eggs, but eggs and immature stages suffer massive mortality (for example, floodwater mosquitoes); K-strategists invest large amounts of time and energy on relatively few eggs and offspring, whose survival rates are high (for example, tsetse flies). The r-strategists grow quickly and are good colonizers of unexploited resources, whereas the K-strategists grow slowly but are successful against competitors and natural enemies.

Conditional Strategies: In the course of a life cycle, an insect shifts between two broad phases, each with its own set of behaviors and priorities: *vegetative*, in which the immature insect is committed primarily to feeding, growth and storage of food, and *reproductive*, in which the adult insect is devoted primarily to dispersal and reproduction. In addition, three tactical alternatives may occur in either phase: *active*, *migrating*, and *dormant*. These are induced by particular environmental conditions. Active insects carry on their vegetative or reproductive functions because conditions allow it. Both the ability to migrate and the ability to become dormant allow insects to exploit temporary resources. Dormancy occurs when the insect remains in place but endures inimical conditions, such as winter, dry season, or unpredictable drought, when growth and reproduction are impossible. Insects may behave in particular ways to prepare for dormancy but are otherwise inactive. During dormancy the insect reduces its metabolic rate and exists in one of two distinctive physiological states: quiescence or diapause (see Chapter 2).

Migratory Behavior: Like dormancy, migration often occurs because of inimical conditions, but in this case the insect escapes in space instead of time, by moving to a better environment. These migrations may be either round trips or one-way trips, and unlike migratory birds, the round trip may be achieved by members of two separate generations. Well-known migrations accommodate either the seasonal deterioration of an insect's resources or the shrinkage or overexploitation of resources. The famous monarch butterfly, *Danaus plexippus* (L.), migration is a seasonal round trip between northern North America, including southern Canada, and its more mild southern reaches. In this migration, dormancy plays an integral part. The southward-flying butterflies are in a state of reproductive diapause during their approximately 3,300-km (2,000-mile) journey, although they continue to feed on nectar. In their main overwintering habitats in coastal California and central Mexico, they are usually torpid but will fly and drink water on warm days. Only in the spring, when they start the northward journey, do they become reproductively active, breeding on milkweed plants. Up to three generations are passed during this more leisurely spring migration. Many other insects that migrate seasonally simply die out at the end of their northern migration as winter approaches, rather than returning south. Quite different are the migrations of the notorious locusts, such as the desert locust, *Schistocerca gregaria* (Forskal), which are species of grasshoppers (Acrididae) capable of developmental dimorphism. They perform a one-way trip with no diapause, no particular destination, no periodicity, and no finishing time. The root of migration is a shrinking suitable habitat, which causes crowding, and mutual stimulation of grasshoppers leads to their transformation from a *solitary phase* to a *gregarious phase*. The complete transformation takes up to three generations, and the gregarious locusts are strikingly colored and behave quite differently from solitary ones. The gregarious forms remain a cohesive unit, even when their swarms number in the tens of billions and cover up to 1,000 km^2. They may travel across continents, eating plants and reproducing as they go. If unchecked, they eventually are carried by wind to regions where rain is falling and forage is growing over wide areas, so they become dispersed and revert to the inconspicuous solitary phase. Locust migrations, known throughout all history, are still a serious problem in Africa and the Middle East. Locusts also occur in China, South America, and Australia. The species that plagued the North American plains in the 1800s is now extinct. Like locusts, when aphids become too crowded on a plant they begin developing wings and migrate to new plants, also a one-way trip. The emigration of some aphids has a round-trip aspect, because they migrate from a spring host-plant species to a summer one, the shift being caused by a physiological change in the spring plant. The aphids return to the spring host species the following year. Tropical army ant (for example, *Eciton*) colonies make impressive daily raids from a central bivouac but are nomads on a perpetual one-way trip. During their *nomadic phase*, the entire bivouac, queen and all, must be moved daily while the larvae are growing, because these carnivores are continually depleting their local resources, mainly insect prey. During their *statary phase*, the bivouac remains in one place, and daily foraging parties extend in all directions for many days. Migration also occurs for reasons other than resource deterioration. Some insects make a round trip between two different kinds of resources that are spatially separated, or simply make a one-way dispersal to colonize new areas. Saltmarsh mosquitoes, such as *Aedes taeniorhynchus* (Wiedemann), which hatch and develop in synchrony after an exceptionally high tide, do both: They go on a spectacular postemergence exodus that results in dispersal, and once they settle, the females translocate between two habitats during each reproductive cycle: They often find their blood meals inland but must return to the saltmarsh to lay their eggs. The swarming dispersal of newly emerged winged termites is an example of a purely colonizing migration.

The Genetic Basis of Behavior

Both instincts themselves and the ability to modify them through learning have a genetic basis. A great many insect behavioral traits are demonstrably heritable, as shown by the methods of classic genetics, such as hybridization and backcrossing, mutation, and artificial selection. Entomologists have explored traits' localized expression in the insect body through the use of sexual mosaics (gynandromorphs) and biochemical analysis, and have demonstrated their molecular basis through genome manipulation. Identifying heritable units that underlie behavior has been difficult. This is partly because behavior itself is not easily fractionated into single elements, each caused by the expression of one or a few genes. Unlike color or some morphological features, which may be expressed through a unitary developmental process, behavior requires the participation of sensory receptors, nervous circuitry, appropriate neurochemical states, and a system of muscles to move body parts. A small difference in the genes that control any of these components can result in a difference in behavior. Research indicates that even in cases where a genetically based difference between two insects can be traced to a specific difference in neural circuitry or neurochemistry, that difference usually is the result of many genes having multiple effects; that is, the trait is polygenic and the genes have pleiotropic effects. Among the traits studied in greatest detail are cricket calls, honey bee food hoarding, honey bee hygienic behavior, and a variety of behaviors in the fly *Drosophila*: geotaxis, larval foraging, odor learning, circadian activity rhythms, sex recognition, and courtship songs. The hygienic behavior of worker honey bees in colonies that are resistant to foulbrood bacteria was found, by backcrossing experiments, to consist of two separate acts, uncapping cells of infected larvae and removing infected larvae from the hive. These behaviors assort independently, and analysis indicates that probably at least three genes are involved.

In some behaviors, researchers have discovered simple one-gene control. In the case of larval foraging, two behavioral types of *Drosophila melanogaster* Macquart have been identified: *rovers*, which wander around on their food, and *sitters*, which travel little. These different types occur naturally, each one being favored by different food conditions. Hybrids between rovers and sitters produce offspring in a 3:1 rover–sitter ratio, suggesting that foraging is controlled by a single gene (*dg*2) and that the sitter trait is recessive. The two behavioral types have been mapped to a single locus on a chromosome. Apparently differences in the gene (that is, its nucleotide sequences in the DNA) result in differences in the way RNA splicing occurs, giving rise to different kinds and amounts of the enzyme protein kinase. Protein kinase affects the excitability of nerve cells, which probably causes food receptors or foraging-movement neurons to fire more rapidly. Experimental transfer of *dg*2 DNA from rovers to sitters causes sitters to behave like rovers. In the case of circadian-clock genetics, researchers have found mutant *Drosophila* strains that differ from the normal 24-hour rhythm of activity by having 28-hour or 19-hour cycles or no cycles at all. Each mutant differs only at the *per* locus and only by a single pair of nucleotides among a large group that codes for a particular protein that differs by a single amino acid. The *per* locus also is responsible for very specific tonal features of the male *Drosophila* courtship song that are important to the female for species recognition and mating speed. These features have been traced to a very small part of the gene. The species-specific songs of *D. melanogaster* and *D. simulans* Sturtevant apparently derive from a difference of only four amino acids in the protein translated from the relevant region of the gene. However, the entire male courtship ritual involves a series of female-oriented and female-behavior–dependent movements: facing, tapping, circling, wing-extending, licking, and mounting. These must involve many other loci, all contributing to properties of the nervous system that allow this sequence to unfold.

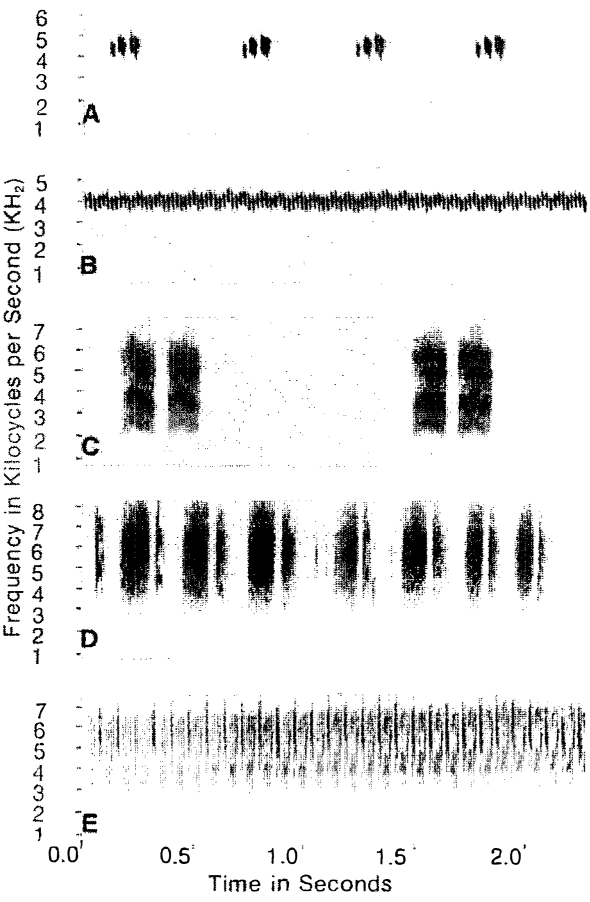
Because behavioral traits, like morphological and molecular ones, are heritable and shared among related taxa, they are used as tools in insect systematics. Despite a reputation for evolutionary flexibility, behavioral characters show approximately the same range, from stability to volatility, as morphological ones. Nest building and courtship displays have been particularly useful, because they are rich in complexity, providing many different traits that can be measured or categorized, independently of one another. Nesting offers the additional advantage of leaving behind, in nest architecture, a permanent record of behavior that can be gathered and stored, even from fossils. Independently of their use in understanding relationships, behavioral characters can be applied to phylogenetic reconstructions based on morphological and molecular data. From them, researchers can infer the evolution of behavior by its appearance and modification among various groups in the evolutionary tree. Similarly, the observation of polymorphic behaviors within one recognized species has led to the discovery of distinct but cryptic species within what then becomes recognized as a species complex.

Behavioral Interactions between Conspecifics

Mating

Sexual Encounter: The vast majority of insect species are sexually dioecious, occurring as either female or male, and most engage in mating, even those whose females have the option of parthenogenesis (see Chapter 2). Mating presents the problem of finding a receptive member of the opposite sex, and insects have two solutions. (1) In *sexual aggregation,* individuals that need to mate convene in special sites, often at certain times of the day or night, during the mating season. These sites may be species-specific places of emergence, feeding, or oviposition, or distinctive landmarks. The aggregations typically have an operational sex ratio strongly skewed toward males, because much of a male's fitness depends on his ability to obtain mates, whereas a female's fitness is distributed more broadly among activities connected with feeding and nesting, and she may have less to gain from multiple matings. Because of their intense competition, the males of many species establish territories that they defend against other males. The territories can have actual value to females for feeding or oviposition, as in the case of dragonflies, or they may be leks, symbolic territories that have no intrinsic value but are sought by females and therefore are prized by males and defended by those with the best competitive ability—for example, Hawaiian *Drosophila* on plant leaves. High-density sexual aggregations over landmarks usually are aerial, the males forming a seething mating swarm that makes establishment of a territory virtually impossible. In that case, competition is based on a male's ability to locate a female quickly as she approaches or enters the swarm, to seize her, and to deny other males access to her before the couple departs. Male-biased mating swarms are typical of many ants and small nematocerous Diptera, such as gnats, midges, and mosquitoes.

(2) In *sexual attraction*, one sex of a species may broadcast a visual, chemical, or auditory signal indicating that the signaler wants to mate, and members of the opposite sex use the signal to find its source. To preclude useless hybrid matings, these signals must be species specific for a given area and season. Visual signals are transmitted in the flashing colors of butterflies' wings in sunlight and in the blinking lights of fireflies' photic organs. In common firefly species, both males and females produce light, the flying male giving a periodic, species-specific calling flash, and the sedentary female answering with a flash from the ground. In this case, it is the female that attracts the male, by answering each of his calls after a prescribed interval, allowing him to locate her. Males of some *Pteroptyx* species, best known in Southeast Asia, gather together in trees along the banks of rivers and flash in unison. This combined effort is thought to be effective in attracting flying females over long distances; at close range, individual attraction still is necessary. Males of some tree cricket and katydid species seem to do the same thing, by synchronizing their calling songs. The best known auditory attractants are produced by cicadas and various Orthoptera, such as crickets and katydids (Figure 4–3). Cicada males buzz by rapidly vibrating two membranes (tymbals) within chambers of the first abdominal segment. The much quieter leafhoppers and planthoppers also use tymbals. Most orthopteran males rely on wing stridulation. A scraper on one wing rubs along a ridged file on the other, causing the wings to vibrate. Some grasshoppers stridulate by rubbing their legs against their folded wings. For typical chemical attraction, as in moths, females release a volatile sex pheromone, which is distinct for each species (even the isomer must be correct) and often is a mixture of two or more chemicals in a specific ratio. Sex pheromones can elicit reactions in males many kilometers from the female caller. As a general rule, males emit attractants that are risky or energetically costly, such as sound, and females emit attractants that are safe and cheap, such as pheromones. Risky attractants are those that predators and parasites can use to locate the sender.



Donald J. Borror

Figure 4–3 Audiospectrographs of some insect sounds. A, Four chirps of the calling song of a field cricket, *Gryllus* sp.; B, A portion of the calling song of the tree cricket, *Oecanthus nigricornis* Walker; C, Two 2-pulse songs of the northern true katydid, *Pterophylla camellifolia* (Fabricius); D, Stridulation sounds produced by the sawyer beetle, *Monochamus notatus* (Drury) (the insect illustrated in Figure 26–75); E, A part of the calling song of the cicada *Tibicen chloromera* (Walker). Frequency is shown here in kilohertz (or kilocycles per second); 4 kHz is approximately the pitch of the top note of a piano.

Courtship: Once males and females have encountered each other, they may proceed directly to copulation or may first engage in various rituals, collectively known as *courtship*. Although both sexes may play active roles, involving two-way communication, usually the male conducts most of the overt performances and appears to be seeking acceptance. Obversely, typically it is the female that rejects a potential partner. These rituals include leg and wing displays (Figure 4–4), dances and songs, the use of silken traps and guides, and various feeding devices. Feeding includes items of food (nuptial gifts), such as prey, secretions from glands on the male's body (so-called aphrodisiac), large and edible extensions of spermatophores, or the body of the male himself. In the last instance, including the widely publicized cases of praying mantises and black widow spiders, the male usually attempts to escape with his life after inseminating the female, and the frequency of sexual cannibalism in nature is disputed. But at least in the Australian red-back spider, the male clearly offers

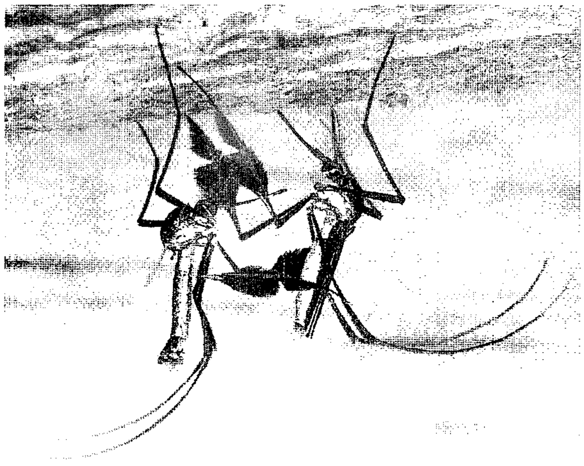


Figure 4–4 Courtship of the neotropical mosquito *Sabethes cyaneus* (Fabricius), which is iridescent blue and silver. Mating consists of three phases: precoupling, superficial genital coupling, and full copulation. Within these phases, the male performs a series of courting stages with overt movements that involve extensive use of the midlegs, which on both sexes have "paddles." The stages always occur in this order: free-leg waving, swinging, waving, and waggling. If the female is receptive, she lowers her abdomen during the swinging stage (shown here), making genital coupling possible. Full copulation occurs right after waving, and it is during the waggling stage that insemination occurs.

himself to be eaten. The male gains from self-sacrifice by contributing to the development of eggs in her body, which may become fertilized by his sperm.

Courtship seems to have a number of purposes. Among arthropods with *indirect insemination*, such as scorpions, some springtails, and silverfish, a dance facilitates the transfer of the spermatophore from male to substrate, then to female. Among predators, such as jumping spiders, a male's signals are thought to inhibit the female's inclination to kill. Courtship interchanges also may allow the female to communicate to the male whether she is receptive, which benefits both sexes by precluding time-wasting, strenuous, and potentially damaging attempts by the male to copulate. The two most common explanations for courtship are species isolation and individual mate choice. If courtship displays are species specific, a female that discriminates among them can avoid mating with males of other species, and thus can avoid laying nonfertile eggs or producing aberrant offspring. Furthermore, if the female can discriminate among male performances within her species, she also has the opportunity to accept or reject particular individuals, according to how fit they seem. Most evidence comes from studies in which females choose large males over small ones. Perhaps body size is among the most important messages being communicated during visual displays, but *Drosophila* research demonstrates that females also select males according to their courtship sounds. Insect body symmetry also is important. Any courtship features may be indicators of underlying fitness characteristics, such as ability to obtain food and resist parasites. Hangingfly females (Mecoptera: Bittacidae) accept more sperm from males that present them with larger gifts of prey, which may indicate not only his size, per se, but his ability to obtain prey. Often the mate-choice pathway appears to have led to the sexual selection for males with exceptionally elaborate appearances and performances that have little to do with a male's health or vigor, but rather confer mainly his ability to sire sons that also are stimulating to females. Furthermore, females that choose such stimulating males are more likely to produce daughters that are stimulated by such males. The combined effect is "run-away sexual selection." An alternative to courtship is male–male fighting, which provides for sexual selection of a different nature. If a female attracts more than one male at a time, she does not necessarily choose among them. Instead, a fight ensues, and the female accepts the winner. Intrasexual selection for fighting ability has resulted in conspicuous horns and large mandibles on male beetles. They serve as weapons against each other, rather than as devices to defend against enemies or to impress females, and probably are detrimental to all aspects of life other than fighting for mates.

Copulation: Copulation and/or insemination are the end result of a successful mating. In some apterygote insects, including many Collembola, not only is sperm transfer indirect, but the male may place spermatophores on the substrate and never encounter the female that picks them up. Yet various forms of noncontact and contact courtship also occur in Collembola. Even copulation, which involves direct transfer of sperm from male to female, may not occur between genitalia but rather between genitalia and some other structures on the opposite partner. This ***extragenital insemination*** is the rule in spiders, in which the pedipalps of males are modified into secondary intromittent organs. A male deposits sperm in these small appendages prior to mating and during copulation introduces them into the female's genital opening. A similar arrangement occurs in Odonata. In this case, the male deposits sperm in an organ at the base of his abdomen so that at the time of mating, he clasps the neck of the female with his primary genitalia at the tip of the abdomen, and she curves her abdomen ventrally forward to clasp his secondary genitalia and receive sperm. This strange configuration is the frequently observed "wheel position" of dragonflies and damselflies. In bed bugs (Hemiptera: Cimicidae) and some relatives, it is the female that has a secondary sexual structure: a cleft and associated organ (spermalege) in the cuticle on the ventral side of her abdomen, which the male pierces with his strong, hooked aedeagus. The injected sperm must migrate posteriorly to reach her reproductive tract. The vast majority of insects mate by genital coupling, in which female and male genitalia become locked together while a spermatophore or free semen is transferred to the female. The entire process may last only a few seconds or may go on for hours, during which time the male may continue with courtship movements. Female genitalia tend to be uncomplicated, whereas those of males exhibit a diversity of structures that vary widely among species. Some of these are devices for clinging to the female (for example, claspers) or for transferring sperm, but many others have no known function. A long-held view is that elaborate male genitalia fit perfectly only into females of the same species, so that species isolation is assured, known as the *lock-and-key hypothesis*. A more recent explanation is that in most insects, these structures, like courtship itself, stimulate females in specific ways so that she may choose to accept or use more sperm from some males than others. These phenomena, referred to as *copulatory courtship* or *internal courtship*, are used in cryptic female choice. This hypothesis would explain why species with polygamous females also have males with more elaborate genitalia, the result of sexual selection.

Mating Systems: The multitude of insect mating systems among insects appears related to the wide species differences in the scarcity and distribution of their resources and thus to the likelihood of encountering the opposite sex, but the evolutionary origins of these systems is not always clear. Monogyny (having one female mate) tends to be high when females are thinly distributed or males are excessively abundant. Some monogynous males guard their mates to prevent cuckoldry, such as lovebugs (Diptera: Bibionidae), which prevent her access to other males by remaining in copula for a long period. Others assist females with parental care of offspring, such as *Nicrophorus* burying beetles (Silphidae) and *Lethrus* dung beetles (Scarabaeidae). Polygyny is common when there is a low male operational sex ratio. When females are concentrated in patches, males either attempt to monopolize them by defending them against other males (for example, yellow dung flies, *Scathophaga*) (Figure 4–5) or by defending territories that contain resources a female needs (dragonflies). When female monopoly is unlikely, because the females or their resources are not concentrated, males typically either establish leks (butterflies) or form massive mating assemblages (mosquitoes) at landmarks. In the latter, no courtship or female choice is evident. From the female point of view, monandry (having one mate) is advantageous, especially if life is short and mating involves time, energy, or risk. But polyandry provides sperm replenishment, allows access to a male's resources and services (nuptial gifts, access to defended food or oviposition sites, protection from aggressive males), and allows the female to diversify the paternity of her offspring or possibly to select sperm from among several matings. The conflict between the best interests of males and females derives from the fact that sperm are numerous and cheap, eggs fewer and expensive. This reasoning leads to the explanation for females' more limited sexual activity, higher mate selectivity, and extensive investment in parental care. Males lose little by making mating mistakes and usually can gain greater fitness by inseminating more mates rather than by helping to rear the offspring of one mate, especially if his paternity is not assured. By extension, the asymmetry be-

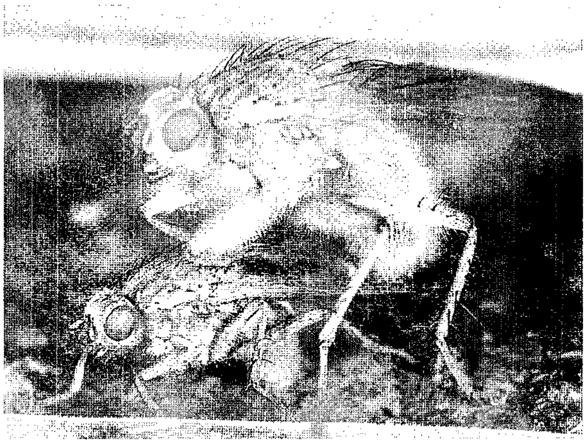

W.A. Foster

Figure 4–5 Postcopulatory mate-guarding during oviposition by the yellow dung fly, *Scathophaga stercoraria* (L.). The polyandrous females oviposit only in fresh ungulate dung, and the larger males aggregate there to mate with them. A gravid female copulates with the first male quick enough to catch her, usually in vegetation close to the dung, then they uncouple genitalia and she proceeds to oviposit on the dung while the male stands over her, fending off sexually aggressive males. If there is a takeover, the female is inseminated by the new male. About 80% of her eggs are fertilized by the male currently guarding her. Thus, the male assures his paternity by protecting the female, and guarding serves both sexes by making oviposition possible.

tween the sex roles also explains why males perform most courtship displays, take the risks, do the fighting, defend territories, and protect the females they mate with. There are a few exceptions to this general sex-role rule. Among giant water bugs (Belostomatidae), females of some species lay their eggs on the males' backs, and the males give the eggs special care until after hatching. A male will not let a female lay eggs on his back unless she first lets him inseminate her, assuring his paternity of the offspring. Females of other giant water bug species lay their eggs on emergent vegetation, and the male guards them there. Another female may attempt to kill the eggs and become his mate, so that he will guard her eggs instead. Mormon cricket females court males, whose mating services are exceptionally valuable because the males produce large, edible spermatophores. A male weighs courting females (by assessing their heft) and mates with the heaviest one. Heavier females produce more eggs, so his choice results in a greater number of offspring sired by him.

Nesting and Parental Care

Insect parents exhibit a broad spectrum of care for their offspring. Some show none at all, such as stick insects that simply drop eggs to the ground beneath the vegetation they are feeding on. But the majority of solitary insects do things that improve an offspring's chance of survival. Usually the female alone does this, but in some cases the male–female mated pair cooperate. The most elementary form of care is oviposition-site selection. Females of plant- and animal-feeding species with narrow host ranges seek hosts on which their larvae will thrive. So do insects that develop in very specific aquatic habitats. Beyond this, some females remain with the eggs, guarding them from natural enemies or physical damage until the eggs hatch, or until sometime later. A further step is taken by insects that create a nest to protect the eggs and immatures, a nest that may be as simple as a hole in the ground or a curled leaf. Others construct elaborate structures and carry out necessary maintenance. Still others provide the immatures with food, either just once or repeatedly as the offspring develop (progressive provisioning). For example, burying beetles work as mated pairs to lower a small, dead bird or mammal into a cavity in the ground and to prepare it as a cuplike nest in which the larvae develop, first feeding them mouth-to-mouth and later allowing them to devour the cup itself. Among solitary wasps that hunt prey for their offspring, a range of species perform various numbers of steps in nest building and prey preparation and provisioning. The most advanced forms stay with their offspring, feeding and defending them and cleaning the nest until they are mature and can fend for themselves.

Social Systems

Insects that form cooperative units have two large advantages over insects that live alone: (1) They are quick to discover and monopolize resources, by communicating the location of food, mounting mass attacks on invaders, and maintaining territories to exclude competitors. (2) They can build large nests rapidly, which protects them and their offspring against natural enemies, harsh weather, and stressful environments, and their close association allows easy transmission of mutualistic organisms.

The rudiments of advanced sociality among groups of arthropods are evident in parental care. In a convenient classification, *presocial* insects are divided into those that are *subsocial*, rearing their offspring alone, and those that are *parasocial*, sharing their rearing with other parents of the same generation. These presocial arthropods include members of many insect orders and also crustaceans and spiders. Each subcategory has gradations that end in *eusociality*. Eusocial insects traditionally meet three criteria: Their groups contain overlapping generations, perform cooperative brood care, and have a caste of nonreproductives, the "sterile caste." Within the subsocial category of presociality are primitive forms that lack complete overlap of generations, intermediate forms whose generations overlap, and advanced forms in which the offspring remain with the group and share in caring for further offspring, including their own. Within the parasocial group, which consists primarily of bees, are primitive species in which females nest together, either gregariously (separate nest entrances) or communally (a shared nest entrance). Tent caterpillars and webworms (both Lepidoptera) sometimes are considered communal, because they build, expand, and repair their protective nest together and cooperate on foraging expeditions. Nevertheless, the group consists only of immatures and thus does not involve parental care. A more advanced parasocial form is *quasisociality*, in which communal nesters cooperate in providing brood care. Still more advanced is *semisociality*, in which the cooperatively brooding adults include some nonreproductives. Yet this group abandons the nest before the emergence of the next generation, and those offspring start new nests elsewhere. Primitively eusocial insects meet all three criteria but there is only one relatively undifferentiated sterile caste, the workers. Progressively more advanced eusocials show more differentiation among colony members, including large differences in form and behavior between reproductives and workers. Colonies of advanced termites may contain several kinds of worker and soldier castes, and advanced ant societies have multiple worker subcastes, including the large majors, the soldiers, medias that do most of the foraging, and tiny minors that never leave the nest.

Insects known to meet the three conventional criteria of eusociality are found only in the orders Isoptera (termites), Hymenoptera (bees, wasps, and ants), and perhaps Coleoptera (beetles). All termites and all ants (Formicidae) are eusocial. Among the wasps, eusocials occur in some Vespidae (all Vespinae, some Polistinae) and one species of Sphecidae. Among the bees, they occur in some Halictidae (some Augochlorini and some Halictini within the Halictinae), and some Apidae (some Ceratini within the Xylocopinae, all Apinae). Among the beetles, one species of ambrosia beetle (Curculionidae: Platypodinae) seems to meet the eusocial criteria. One noninsect arthropod is eusocial: *Synalpheus* pistol shrimp (Decapoda: Alpheidae), whose colonies live in sponges. Among vertebrates, the only clearly eusocial animals are the naked mole rats (Rodentia: Bathyergidae), whose underground societies roughly parallel those of termites, except that the rats may have several reproductive males ("kings").

The preceding scheme of presocial and eusocial insects is not entirely neat. Aphids, which usually seem oblivious to one another on a plant stem, in some cases release an alarm pheromone when attacked, causing others in the group to save themselves by dropping off the plant (Figure 4–6). Communal caterpillars live much like a society as they develop, but they cannot reproduce, and adults are solitary. Australian gall thrips, which live as family groups of multiple generations inside plant galls, have an anatomically distinct soldier caste, as do some advanced eusocial insects, but the flightless soldiers are not sterile. And cottonwood gall aphids do have a sterile female soldier caste to defend the all-female family in the gall, but there is no cooperative brood care. Brood care is a necessity chiefly of holometabolous insects that have larvae unable to feed themselves. Furthermore, members of a sterile caste of many eusocial insects are not permanently sterile but may assume reproductive duties if needed (as discussed later in this chapter). Delayed reproduction of adults, overlapping generations, and cooperative brood care are not uncommon in groups of other kinds of animals, including birds and mammals, so the demarcation between presociality and eusociality can be blurred. Yet these other animals lack fixed morphological caste distinctions, so they can be considered primitively eusocial at best. Despite its imperfections, the social classification provides a useful tool for understanding how advanced sociality in insects may have arisen. Living examples of degrees of subsociality and parasociality demonstrate alternate routes to eusociality from different directions. A third, the *polygynous family* route, proposed for some Hymenoptera and perhaps applicable to spiders as well, combines features of each, progressing from intermediate or advanced subsociality to quasisociality as females from different generations cooperatively tend their brood.

Entomologists have used three basic ideas to explain the emergence of societies, particularly to address the evolutionarily counterintuitive origin of self-sacrificing sterile castes by natural selection: (1) In *mutualistic aggregation,* group living and reciprocal altruism benefits all members, especially under certain environmen-

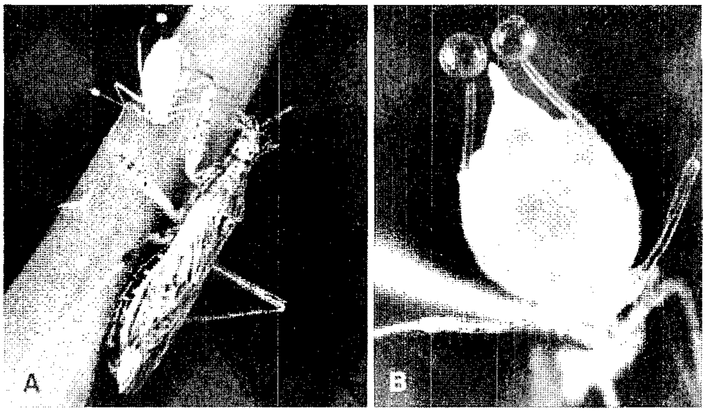


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Figure 4–6 A, A damsel bug, *Nabis americoferus* Carayon, attacking the aphid *Acyrthosiphon pisum* (Harris), and the aphid secreting cornicle droplets in response to the attack. **B**, Secreted droplets on the tips of the cornicles of the aphid *Acyrthosiphon solani* (Kaltenback).

tal conditions; only one or a few reproduce, yet all have a chance to become reproductive at some time. (2) In *parental manipulation*, the reproductive individual (the queen) controls the nutrition of her helpless larvae, so by restricting their food, she diminishes or eliminates their reproductive capacity. (3) In *kin selection*, members of the group are closely related, so nonreproductive members gain *inclusive fitness* (genetic propagation) from the success of their reproductive relatives. The third idea offers an attractive explanation for the fact that eusocial, female-dominated societies have evolved at least 12 times among Hymenoptera, which all have an uncommon method of sex determination: Males develop from unfertilized eggs and are haploid; the females develop from fertilized eggs and are diploid. Because of this arrangement, hymenopterans have pedigrees in which, on average, full sisters are more closely related to each other (0.75) than to their own female offspring (0.5) or their brothers (0.25). This means that a female hymenopteran can indirectly propagate her genes quite efficiently by self-sacrifice that directly or indirectly benefits her reproductive sisters. However, this one type of selective pressure favoring altruism does not account for eusociality in insects in which both sexes are diploid, notably termites. Researchers have suggested a similar inclusive fitness mechanism for termites, the result of alternating periods of inbreeding and outbreeding, as well as several ecological factors. Even in Hymenoptera, it is plausible that all three proposed mechanisms have been involved. One researcher has proposed that these three mechanisms be integrated into an appealing scenario consisting of five stages: colony mutualism, gambling for reproduction, parental manipulation, kin recognition and selection, and the superorganism. In the final superorganism stage, the colony may be thought of as the unit of selection, a single organism whose sterile castes are merely cellular extensions of the queen's body and whose new reproductives are her gametes. A major difference, however, is that the individuals within an insect colony are not genetically identical, which reveals itself occasionally in conflicts of interest. For example, a honey bee queen mates multiple times, so her worker offspring come from different fathers and are not all related by 0.75. Workers with the same father (full sisters) cooperate with each other better than with half-sisters.

Social Communication

Members of insect societies communicate by volatile pheromones, contact stimulation (both pheromonal and mechanical), and sound. The messages that act as *releasers* of behavior communicate alarm, attraction and assembly, recruitment, and recognition. Those that act as *primers*, most of them pheromones, either stimulate or inhibit development into a particular caste or prevent particular behaviors from being expressed. Primer pheromones commonly are transmitted during trophallaxis, the exchange of food and secretions, or during grooming. Mouth-to-mouth trophallaxis is typical of Hymenoptera, whereas termites transfer many materials through their feces, and communication is therefore anus-to-mouth trophallaxis. The best understood recruitment systems are trail making in ants and dancing in honey bees (discussed later). Contact chemicals are important in allowing a worker to identify the stages and castes of its nestmates and to recognize dead nestmates. In addition, the ability to recognize nestmates in general is universal among social insects. The characteristic odor of each colony is carried on the insect and appears to involve both genetic and environmental factors. An individual entering another nest, even if of the same species, generally is attacked.

Social insects often work together to accomplish extraordinary tasks that suggest planning and insight. Honey bees are recruited to the best sources of nectar, shape the cells of their wax combs into structurally ideal hexagons, and thermoregulate their hives; ants take the shortest routes to food, make flanking movements during raids, and build neat walls of uniform thickness to seal the nest; termites build underground arches that meet in the middle; weaver ants cooperatively pull leaves together so that others, holding silk-producing larvae, can bind them (discussed later). You might infer that all these activities require either understanding of the larger goals or an exceedingly complex system of communication, entailing explicit instructions from a leader or detailed information passed back and forth among individual members. Yet a close examination of individuals engaged in cooperative activities often reveals a fine level of disorder and apparent chaos. Effectiveness emerges at a higher, statistical level, through mass action. Studies indicate that even the most clever and efficient activities are performed by individual workers following very simple behavioral rules, through a process of self-organization. Communication simply meshes the behaviors in particular ways to make this possible.

Comparison between Termites and Eusocial Hymenoptera

The eusocial societies of termites and hymenopterans are fundamentally different because only the latter have complete metamorphosis and are female dominated. The developmental instars of termites are functionally similar to the adults. After one or two molts, termites can fend for themselves, and in one form or another both sexes of immatures do most of the work of the colony. Typically, termites have a single reproductive pair, a king and a queen. Hymenopterans, in contrast, have helpless larvae that usually contribute little or nothing to the colony, so various forms of female adults do all the work. Adult males also contribute nothing and are present only during mating periods. As a general rule, there is a single reproductive, the queen.

Most termites are pale or white, whereas ants tend to be yellow, red, brown, or black, and have a narrow constriction at the base of the abdomen. Yet termites and many ant species share superficial similarities, such as having colonies that last for years, royalty that shed their wings, workers that never have wings, soldier forms, and a readily visible reproductive exodus swarm. Their nests often are constructed of "carton" (made of dead plant materials, feces, or soil) or are located in protected cavities in tree trunks, logs, or underground. These similarities give rise to the termite misnomer "white ants."

Termite Societies

Termite colonies may be completely underground, in earthen mounds that rise above ground, on or inside dead wood (human habitations included), or high in living trees, depending on the species (Figure 4–7). They function for years, sometimes decades. All species need dead plant material as food. Their ability to use this food effectively depends on a mutualistic relationship with internal bacteria or protists, or with cultured fungi. The nest consists of chambers and tunnels formed from mud, plant material, and fecal pellets. The specific chambers are dedicated to housing the king and queen (royal chamber), the brood, plant material, or a fungus garden. The tunnels serve as conduits between chambers or as heat chimneys and air circulators. Even on open surfaces, such as tree branches or the side of a house, termites typically travel in covered passageways. The various body forms in a typical colony fall into two categories: *nonfixed castes* and *fixed castes*. Nonfixed castes are developmental stages, that is, nymphs (but called *larvae, pseudergates, presoldiers,* and *nymphs,* depending on developmental state), that serve as unfixed workers and eventually can molt into one of the fixed castes (workers, soldiers, primary reproductives, or supplementary reproductives). Members of fixed castes molt no further. Workers and soldiers may be viewed either as developmentally arrested immatures or as sterile adults. The workers are devoted to constructing and repairing the nest, nursing larvae, feeding the royal pair, and foraging for plant matter. Soldiers protect the colony by attacking invaders. Their modified heads are used either to grasp enemies in their large mandibles (mandibulate soldiers) or to squirt them with noxious or sticky substances from a gland on the front of the head (nasute soldiers). In some species, the soldiers can do both. Lower (primitive) termites lack a fixed worker caste, and all stages and castes are divided equally between females and males. Some advanced termites may have two or more kinds of fixed worker and soldier castes, each consisting of males or females only. Colonies of some termite species often contain more than one reproductive female, especially when the colony is large and diffuse.


A.M. Vargo

Figure 4–7 Visible portion of subterranean-based *Cubitermes* termite colony in equatorial Africa. The architecture apparently is designed to shed water during the heavy rains, yet allow exhaust of stale air and intake of fresh air, by convection.

New termite colonies are founded when brachypterous nymphs (that is, nymphs with externally visible wing buds) in mature colonies molt by the thousands into alates (winged adults that are future primary reproductives) and leave the nest at the same time as those in other colonies in the area. These exodus swarms occur typically during the onset of a warm or wet season, triggered by a heavy rain. After a period of weak flight, the alates land on the ground, males locate females by a female pheromone, both shed their wings, and the pair crawling in tandem quickly locate a site for a new nest. The newly established primary reproductives (king and queen) begin to rear offspring, but it may take several years before their own colony can produce alates. In the meantime, larvae are developing into pseudergates (unfixed workers that can remain uncommitted to a fixed caste), presoldiers and soldiers, brachypterous nymphs, or supplementary reproductives, depending on the needs of the colony. In well-defined colonies of primitive termites and many advanced ones, a supplementary reproductive with functional gonads appears only if the queen or king dies, the replacement having molted from an older larva, pseudergate, or nymph. Otherwise, separate primer (development-controlling) pheromones from the king and queen are passed via their feces to all members of the colony by their anal–oral communication system, preventing unfixed termites of each sex from taking over reproductive duties. If substitution accidentally occurs, or if several supplementary reproductives appear at once, a contact pheromone from the oldest reproductive causes workers to kill the others. An inhibitory primer-pheromone system apparently also keeps soldiers at a small but constant proportion of the total number of colony members.

Paper Wasp Societies

Paper wasps build their nests from a mixture of wood fibers and saliva, pressed by their mandibles into thin sheets of paper that make up both the general nest structure and the comb of hexagonal cells in which they rear their brood (Figure 4–8). These cells typically are inverted, so the larva growing in each is oriented head-downward. In common *Polistes* wasps of North America, a single comb is attached to the underside of an overhanging substrate (commonly the eaves of houses in residential areas) by one or more pedicels. In yellow jackets and hornets (for example, genera *Vespa*, *Vespula*, *Dolichovespula*) and also many tropical paper wasps, many combs are attached one below the other, and all combs together are enclosed within several layers of paper, perforated by an opening for adult wasps to pass in and out. These enveloped, multitiered nests may be attached to tree limbs or overhangs or be situated in rock piles or underground with a tunnel leading to the surface. During most of the season of nest growth, the colony consists of a queen and numerous slightly smaller female workers. The queen spends most of her time at the nest, laying eggs. The workers lack functional ovaries. They collect wood fibers, expand the nest, forage for nectar, meat (prey or carrion), and water, and defend the nest against intruders, using a venomous sting. There is some tendency among workers to specialize in certain tasks, but they are capable of doing any of them. The helpless larvae contribute to the colony only by supplying nutrients to the adults by trophallaxis.

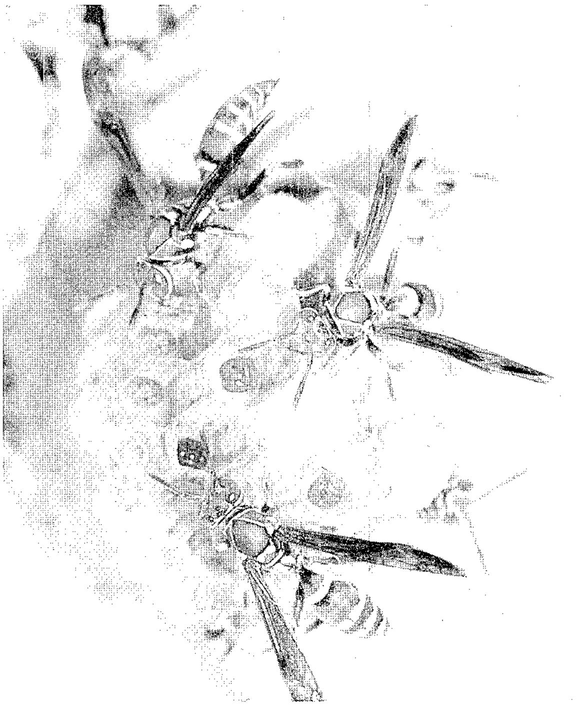
H. Briegel

Figure 4–8 Nest of the paper wasp *Polistes exclamans* (Viereck), with nearly identical foundress (queen), subordinate foundresses, and workers. Centrally located nest cells with white caps contain pupae; open cells closer to the periphery are uncapped and contain growing larvae. In one cell, an unhatched egg is visible.

New colonies are founded by inseminated females destined to be queens. In temperate climates, these foundress wasps overwinter in sheltered sites, either in a cluster (*Polistes*) or in isolation (for example, *Vespula*). In the spring they start new nests (old nests are rarely used) by themselves. *Vespula* foundresses always perform all foraging, construction, egg laying, feeding, and defending duties until the first workers emerge as adults. *Polistes* foundresses sometimes are joined by one or two females from the same generation, which assume the rank of subordinate foundress with nonfunctioning ovaries and perform the tasks of workers. If at any time the foundress dies, one of the subordinates will rejuvenate her own reproductive system and become the new queen. During colony growth, fertilized eggs are laid in worker cells and receive only moderate amounts of food. Near the end of the season, the queen begins laying unfertilized eggs, which develop into males, and fertilized eggs in cells slightly larger than those of workers (in the case of *Vespula*), which develop into foundress daughters. The latter receive more food than workers and become larger adults. Males await foundress daughters near nests or potential overwintering sites, but all males are dead by the time foundress daughters are safely sequestered. In subtropical and tropical regions, paper wasps may have many foundresses and maintain nests for much longer periods of time, with periodic queen replacement and seasonal production of reproductives for dispersal.

Ant Societies

Ant species form nests in a wide variety of sites: deep under ground, beneath rocks, inside old logs, inside hollow branches, inside chambers provided by mutualistic plants (see discussion of myrmecophytes later in this chapter), and high in trees. Some construct their nests of carton, others from living materials, such as the leaf nests of weaver ants (*Oecophylla*), which are held together by silk, from larvae, that workers manipulate in a stitching action, just prior to forming cocoons. The nomadic army ants (such as *Eciton*) and safari or driver ants (such as *Dorylus*) form a temporary nest from the interlocking bodies of living workers. Nests of solid construction may have tunnels and chambers devoted to the queen, brood, food, or fungus gardens. A typical growing colony has one wingless queen and numerous wingless female workers. Some ant species, especially those with large and dispersed colonies, may have secondary reproductives (worker–queen intermediates that lay eggs) or multiple queens. Workers may be all of one type or may be divided morphologically into several subcastes with different functions: *Minors* are small and often remain within the nest, cleaning and tending to the brood; *medias* are of intermediate size and do most of the foraging; *majors* (often referred to as *soldiers*) are large-bodied, with exceptionally large heads and mandibles, and defend the nest or columns of foraging workers. In the case of nomadic ants, majors also guard the procession of all colony members (many carrying a larva) as they move to a new bivouac. The foods of ants are extremely diverse. Harvester species collect seeds and store them in chambers. Honeydew collectors are closely associated with honeydew-producing Hemiptera (discussed later), in some cases storing the fluid underground within the bodies of designated workers (honeypot ants). Carnivores may be either generalist or specialist predators, capturing mainly arthropods. Fungus gardeners (the leafcutter ants, tribe Attini) cut fresh leaves and petals from shrubs and trees and place them in chambers where fungus is cultured (see later). Slave makers specialize in raiding or taking over the nests of other ant species and using the labor of the conquered workers. Nest parasites maintain their entire colonies within the nests of other ant species, often lacking a worker caste altogether and depending on the host for defense and food. Most kinds of foraging ants use trail pheromones to lead other foragers to a source of food. A forager that has found food leaves a trail on the substrate as she returns directly to the nest (having used the sun compass to keep track of her position relative to the nest), then recruits other ants to follow the trail. Each ant that finds the food adds to the trail on her return, but when all food has been removed the trail no longer is reinforced and soon disappears.

Colonies of ants typically start like those of paper wasps: periodic production and dispersal of a new generation of reproductives. At a particular season winged adults of both sexes leave the colony, the males form aerial mating swarms that females enter to find a mate. Inseminated females, destined to become queens, shed their wings and find a site to establish a colony on their own. A queen begins by laying eggs and feeding the larvae from her metabolic stores to develop a generation of workers. As the worker base expands, the colony becomes self-maintaining by foraging for food, feeding the larvae, and leaving the queen to egg production. After several years, the colony is sufficiently large that winged males and reproductive females are produced and exodus flights occur. Another type of colony formation, seen in army ants, is division of the parent colony into two groups, one with the old queen and one with a few new, uninseminated female reproductives. All but one are removed from the new colony and allowed to die. The remaining new queen is inseminated by males from her own or other colonies. Control of female caste generally is pheromonal-nutritional. The queen produces a pheromone that prevents workers from feeding female larvae a royal diet until the time of winged exodus approaches, when she also lays unfertilized eggs that will be fed a male diet. Larval diets that allow development of various female subcastes are determined by the needs of the colony, also presumed to be mediated by pheromones.

Honey Bee Society

Honey bee (*Apis mellifera* L.) colonies have been assisted or maintained by humans for thousands of years, to obtain their stored honey or promote their pollinating abilities, which are extremely important to agriculture. Consequently they are the most intensively studied and best understood of the social insects. In nature, nests are established in rock and tree cavities that have a narrow opening. In cultivation, colonies are maintained in baskets or wooden boxes (referred to as *hives*) with similar features. The nest consists of a series of parallel combs, differing from those of paper wasps in that the combs are made of wax and are vertical, so that the cells are horizontal and occur on both sides of the comb. Furthermore, the cells are used not only for rearing brood but also for storing honey (concentrated flower nectar) and pollen. In addition, the combs serve as platforms where workers exchange food and information. The colony consists of one winged queen, a few hundred winged males (drones), and many thousands of smaller winged female workers. The queen is entirely dedicated to producing eggs and laying them in cells. Drones are present only during the reproductive season, contribute nothing to the colony, and serve to mate with new queens from other colonies. Workers generally follow a sequence of tasks and associated gland activity: (1) cleaning cells; (2) feeding larvae salivary secretions (known as *bee milk* or *royal jelly*) and pollen mixed with honey (bee bread); (3) building cells, using wax from their abdominal wax glands; (4) storing pollen and honey, which has been taken from incoming foragers; (5) guarding the colony, by remaining near the entrance and attacking intruders with a suicidal sting; and finally (6) foraging, which includes collecting nectar, pollen, resins, and water, up to 8 km from the nest (Figure 4–9).

Communication among workers includes the release of an alarm pheromone from the sting apparatus, which remains in the intruder and attracts other workers to the site of the sting and induces further stinging. An assembly pheromone, released by a forager after returning from a successful expedition, causes other foragers to gather around to obtain information about the food source. Much of this information is transmitted during a dance, which has components suggesting symbolic language. The dance language differs slightly among different races of honey bee. The following dialect applies to the Carniolan race of northern Europe: When food is less than 20 meters from nest, the forager performs a *round dance*, in which it walks in an almost complete circle, alternating between clockwise and counterclockwise directions. This pattern indicates that the source is nearby, its richness is indicated by the duration and vigor (vibrations) of the dance, and its odor is imparted by the dancer. Between 20 and 80 meters, a transitional *sickle dance* is performed, which contains elements of the waggle dance. Foragers do a perfect *waggle dance* when food is more than 80 m away. It consists of alternating left and right semicircles, with a straight *waggle run* in between, in which the bee vigorously wags its abdomen from side to side while walking forward. Richness and odor of the food source are transmitted as in the round dance. The approximate distance to the food is indicated by the duration of the waggle run, and consequently the number of waggles in it and number of waggle runs per unit of time. The direction to the food is indicated by the angle between the direction of the waggle run and the vertically upward direction. This angle represents the angle between the food source and the sun's azimuth, which is the sun's coordinate on the horizon. The dance occurs within an almost completely dark nest on a vertical surface, so recruited workers detect its geometric features entirely by mechanical stimuli coming from the dancing bee, which they follow during the course of her dance, and from their sense of gravity. The most abstract feature of this communication is the representation of the real sun's azimuth on a horizontal landscape by the direction "up" on a vertical dancing platform.

New honey bee colonies are founded when a large one divides into two parts. The process starts when workers start building queen cells, large cells that hang vertically off the face of ordinary honeycomb, and rearing future queens in them. Typically, the old queen leaves with about half the workers in a *prime swarm*, a mass of bees that comes to rest on a tree branch or other aerial site. By using the surface of this cluster of bees, permanent nest-site foragers employ the waggle dance to recruit each other to cavities that might be suitable, and those dances reporting the best site gradually recruit more workers until a critical mass agrees. Then they all leave together with the queen to relocate

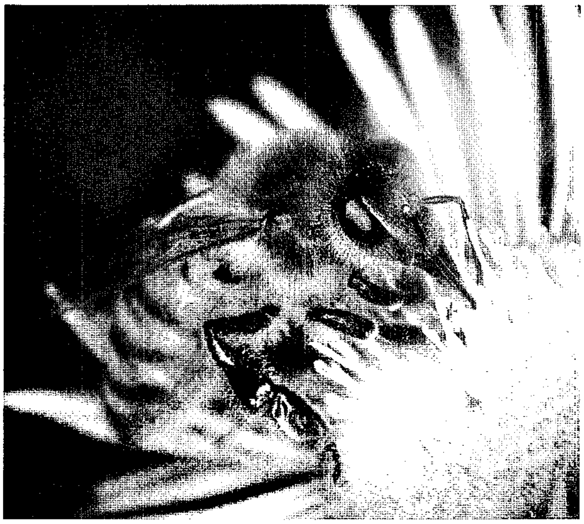
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Figure 4–9 Foraging worker honey bee, *Apis mellifera*, gathering nectar and pollen from a flower.

in the chosen cavity. Meanwhile, at the old nest, the first new female reproductive to emerge destroys the other queen cells. If two emerge at about the same time, they fight to the death, using their venomous stings, so that only one remains as queen. This reproductive female then goes on a mating flight (nuptial flight) to a location high in the air where drones are active. She attracts them with a pheromone and mates with 10–15 in succession, a process that tears the genitalia off the abdomen of each male and causes his death. When filled with a lifetime's supply of sperm, she returns to the nest to begin laying eggs to replenish the stock of workers. In temperate climates, swarming occurs in late spring and may involve two or three *afterswarms*, following the prime swarm. An afterswarm consists of another large proportion of workers and the new queen, who will be replaced by a subsequent queen still developing.

Female caste control is pheromonal-nutritional. As in other hymenopterans, drones are derived from unfertilized eggs, which the queen lays in moderately large cells near the corners of the combs. Workers develop from fertilized eggs in small cells, identical to those used to store food, typically in the central part of the comb. They are fed royal jelly (nurse bee saliva) during the first three days of development, then a steady diet of bee bread. Future queens, in contrast, are fed large amounts of royal jelly throughout larval life. If the resident queen dies, workers hastily build queen cells and transfer diploid eggs from worker brood cells to the queen cells, so that new queens can be reared. (In the *capensis* race, workers, lacking sperm, nevertheless can produce diploid eggs on their own.) The nurse bees decide which diet to give a larva by assessing its development and the kind of cell it is developing in. Ultimately, it is the queen who controls caste, by releasing an inhibitory mandibular-gland pheromone ("queen substance") that is passed through the colony and prevents workers from building queen cells. Entomologists think that during swarming season either the colony has grown so large that the pheromone becomes too dilute to be effective or that the queen herself reduces its production, so new female reproductives can be produced.

Community Associations

Arthropods in general are major players in all biotic communities. In the marine environment, crustaceans have large roles, whereas on land and in freshwater, insects are dominant but are virtually absent in marine communities. Exceptions are a few insect species on the ocean's surfaces and along marine beaches and the intertidal zone. Green plants are the universal producers of organic materials, using energy derived from the sun. Phytophagous (herbivorous) arthropods feed on plants to obtain these materials and are thus primary consumers. Zoophagous arthropods are secondary, tertiary, or quaternary consumers, feeding at some more distant link in the *food chain*, either on animals that feed on plants or on animals that feed on other animals. Detritivores feed on dead matter at any of several trophic links, further using the organic materials there. Some insect detritivores are omnivorous, feeding opportunistically on living plant or animal tissue as well. At each step in the transfer of food from consumed to consumer, roughly 90% of the energy contained in the food is lost. Thus the total amount of biomass among primary consumers is large, but at the top of this *trophic pyramid* the biomass is small. This means the environment sustains a greater mass of herbivores (grasshoppers and buffalo) than carnivores (lice and eagles). Actual relations among members in a community do not form a simple pyramid based on a few food chains. Rather, they usually form a *food web*, with each species either eating or being eaten by several other species (Figure 4–10). This is because in every feeding category, species vary along a continuum of food preferences, from extreme generalists to extreme specialists. Furthermore, not all relationships involve just eating and being eaten. The exact nature of the relationship between one insect species and other organisms, whether based on food and or another vital resource, defines its ecological role, or *niche*. By convention, in *mutualism* both organisms benefit from the relationship. In *commensalism*, one benefits and the other is unaffected. In *parasitism*, the small organism (the parasite) benefits and the large one (the host) is weakened. In *predation*, the large organism (the predator) benefits and the small one (the prey) is killed. Between parasitism and predation, there are *pathogens* (bacteria, protozoa, nematodes, fungi) and *parasitoids* (insects), which are small parasites that seriously harm or gradually kill the larger host. The term *symbiosis* is reserved for the physically close and long-lived relationships observed in mutualism, commensalism, and parasitism.

Microbial Relationships

Mutualists: A variety of microbes assist insects nutritionally, living in close association with them or internally. In return, the insect provides a home, a source of food, and a mechanism for transmission to other insects. Many wood-eating termites, and also wood-eating cockroaches, harbor colonies of flagellate protists and bacteria in a special chamber in the anterior hindgut. These microbes break down cellu-

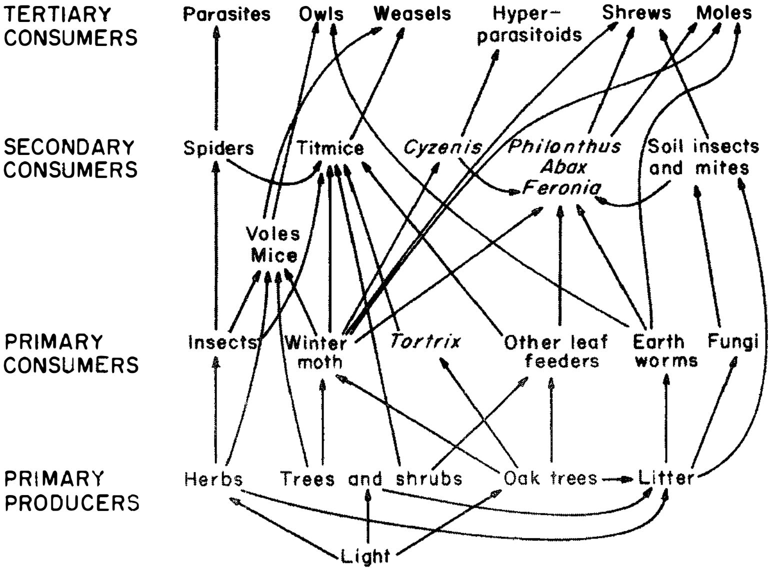

Figure 4–10 Major feeding links within a community in one English woodland, illustrating the general nature of food webs and the integral roles of insects in them. *Tortrix* is a moth, *Cyzenis* is a tachinid fly, *Philonthus* is a staphylinid beetle, and *Abax* and *Feronia* are carabid beetles.

lose, which is otherwise indigestible. They are passed to newly hatched termites by the fecal–oral transmission route used also in communication. Similarly, wax moths, which live in honey bee colonies and eat the wax of their honey combs, contain bacteria that digest the wax. Other insects maintain colonies of bacteria that provide vital nutrients, such as vitamins. These bacteria may be maintained in gut crypts or intracellularly in mycetocytes, which form a special structure, the mycetome. For example, insects that feed on vertebrate blood during their entire life cycle (kissing bugs, bed bugs, lice, tsetse flies) obtain insufficient B-vitamins from the blood, but the bacteria in their guts or mycetomes provide these vitamins. The bacteria are passed to new generations via eggs or feces.

Some termites and ants grow mutualistic fungi in gardens as a source of food, and in return the insects provide the fungi with a substrate for growth and with transmission mechanisms. Advanced termites (Macrotermitinae) grow *Termitomyces* fungi in special chambers on combs of fecal pellets containing plant fibers. The termites eat both combs and fungus, which contain cellulases allowing digestion. Leafcutter ants (Attini) grow various basidiomycete fungi on a mulch of freshly cut leaves and flowers and eat the swollen tips (gongylidia) of the hyphae. The ants also keep the mutualistic fungus from being destroyed by a parasitic fungus. In both kinds of fungus-growing insects, new reproductives that leave the parent colony carry the fungus with them, to seed a new garden. Some bark beetles (Scolytinae) and ambrosia beetles (Platypodinae) also cultivate fungi (Ascomycetes and Fungi Imperfecti) in their tunnels beneath tree bark and eat special growth forms.

Pathogens and Parasites: Insects are attacked by a wide variety of microorganisms, including viruses, rickettsiae, spirochetes, eubacteria, protists, and fungi. Insects also are infected by flukes, tapeworms, roundworms, hairworms, thorny-headed worms, and parasitic insects (see discussion later). Most of these infections result in death of the host insect and form the basis of several kinds of successful biological control of insect pests.

Arthropod Vectors of Pathogens and Parasites: Arthropods often serve as vectors, transmitting pathogens and internal parasites to vertebrates or to plants. The most important vectors of human and livestock diseases are mosquitoes and ticks. Some pathogens are transmitted accidentally or incidentally, having no biological relationship with the arthropod (*mechanical transmission*), for example, a variety of viruses and bacteria carried by house flies and cockroaches. In closer vector–pathogen relationships (*biological transmission*), which are obligate and fairly species specific, the parasite completes its *extrinsic cycle* in the vector, by multiplying (*propagative*), multiplying and transforming (*cyclopropagative*), or only transforming and growing (*cyclodevelopmental*). Propagative pathogens include viruses, rickettsiae, spirochetes, and eubacteria. Cyclopropagative pathogens include sporozoan and flagellate protists. Cyclodevelopmental parasites include flukes, tapeworms, roundworms, and thorny-headed worms. Many of these cause serious diseases in humans and livestock, affecting hundreds of millions of people. On a global basis, among the most noteworthy livestock and pet diseases (and their vectors) are babesiosis (ticks), theileriasis (ticks), nagana (tsetse flies), equine encephalitis (mosquitoes), and dog heartworm (mosquitoes). Among the most infamous human diseases are malaria (mosquitoes), river blindness (black flies), elephantiasis (mosquitoes), encephalitis (mosquitoes), Lyme disease (ticks), spotted fever (ticks), dengue (mosquitoes), epidemic typhus (lice), relapsing fever (lice and ticks), Chagas disease (kissing bugs), yellow fever (mosquitoes), sleeping sickness (tsetse flies), leishmaniasis (sand flies), and plague (fleas). Most arthropod vectors are blood feeders (discussed later), offering the pathogen or parasite an easy way to pass between vertebrate and invertebrate hosts without exposure to the outside environment, but there are many variations in the exact manner of host inoculation. These include vertebrate autoinoculation with the crushed vector or its feces or inadvertent ingestion of the infected arthropod. Within the vertebrate, the pathogen completes its *intrinsic cycle* and then is infectious to the arthropod again. This alternation between hosts is called *horizontal transmission*. By contrast, some propagative pathogens also are transmitted from generation to generation of arthropod by transovarian transmission, that is, *vertical transmission*. This helps maintain the chain of infection in the face of vertebrate immunity and conditions when horizontal transmission is impossible, as during winter.

When referring to arthropods that act as vectors of plant pathogens, plant pathologists speak of *nonpersistent* and *persistent* pathogens, instead of mechanical and biological transmission, but the meanings are similar. Viruses, phytoplasmas, spiroplasmas, and bacteria are common and economically important pathogens of plants that multiply in their insect vectors. Fungi are typically carried mechanically. Most vectors are thrips, aphids, leafhoppers, planthoppers, and similar insects that pierce plant tissue with haustellate mouthparts, but several kinds of beetles also transmit important disease organisms. Among the well-known vector-borne diseases of crops (and their vectors) are sugarcane mosaic (aphids), cucumber mosaic (aphids), wound tumor (leafhoppers), sugar beet curly top (leafhoppers), aster yellows (leafhoppers), corn stunt (leafhoppers), rice stunt (planthoppers), tomato spotted wilt (thrips), cotton leaf curl (whiteflies), cucurbit wilt (cucumber beetles), and Dutch elm disease (bark beetles).

Plant Relationships

Pollination: The best known of the mutualistic plant–insect relationships is cross-pollination of angiosperms by insects that visit flowers. This service is much more efficient than windborne pollination and is thought to have brought the angiosperms to plant dominance, as well as to diversify the insects associated with them. The most speciose orders of insects—Coleoptera, Hymenoptera, Diptera, and Lepidoptera—also are those that do most of the pollinating. Basically, the insects transfer pollen between plants by picking up pollen from anthers of one flower and depositing it on stigmas of another. In most cases, this activity is purely incidental on the part of the insect. The primary incentive for insects is food provided in the flower: nectar, a secreted solution of sugars with a variable amino acid component, and excess pollen, a valuable source of protein and lipid. This reciprocity has led to a variety of special features of both pollinators and plants. Insects have body modifications for handling the pollen and storing the nectar, and behavioral refinements that help them quickly locate and exploit sources of nectar and pollen: ability to learn and discriminate among colors and scents, an accurate time sense, flower constancy on each foraging expedition, and a tendency to specialize on just one kind of plant (monolexy). These insect behavioral characteristics are promoted by, and benefit, the plants. Plants, in contrast, have evolved features that assist the insect in locating the nectar and that at the same time facilitate pollen transfer: fragrance, colorful petals, nectar guides (petal arrangements and markings), landing platforms, reliable and synchronous flowering times and nectar flows, mechanical pollen-transfer devices, temporary insect traps, and defenses against nectar robbers. Blue and yellow flowers tend to be visited by bees, orange and red flowers by butterflies, and white flowers by moths or generalist short-tongued pollinators, such as flies and beetles. Flowers often promote monolexy by secreting nectar into a corolla that can be reached only by an insect with an exceptionally long proboscis. Some plant–pollinator relationships are particularly close, involving insect development within the flower. In the case of the yucca moth (Prodoxidae: *Tegitecula*), the female gathers a pollen ball in her tentacles (prehensile palps) on one flower, then flies to another, lays her eggs in its ovary, then places the pollen ball on the flower's stigma so that seeds will develop, some to be eaten by the moth's larvae. Fig wasps (Agaonidae) are even more complex. Both sexes of wasp develop in the ovaries of modified female (neuter) flowers of fig trees (*Ficus*) within the fig's "fruit" (the *syconium,* a large receptacle lined with flowers). The wingless males come out first and mate with females while they are inside their cocoons. A female leaves the fruit while it is in the male flowering phase, so that she picks up pollen. She then finds a fruit that is in the female phase and pollinates normal female flowers while ovipositing on the neuter ones. The normal, fertilized flowers develop seeds. In some species of figs, predominantly male, female, or neuter types of fruit occur at different times of year. Commercial Smyrna figs lack wasps and must be pollinated by wasps from "goat figs" that growers place in the orchards, in order for the fruit to develop its thick, edible flesh.

Not all flower visiting and pollination is mutualistic. Nectar-robbing bumble bees that cannot reach the nectar of specialized flowers with their mouthparts cut into the side of the corolla to take the nectar without contacting anthers or stigmas. Nectar thieves merely take accessible nectar but lack the appropriate equipment or behavior to transfer pollen. In the reverse situation, plants employ deception to achieve pollination without providing the insect with anything in return. Flowers that release odors similar to rotting flesh or excrement attract saprophagous flies and beetles, which pick up or deposit pollen while wandering around on the flower. Blow flies that are attracted to the star flower (*Stapelia*) even lay their eggs at the center of the flower, where the hatched larvae die. Many of these flowers are brown or purple, and the dead-animal effect may be enhanced by simulated hairs. Ground orchids in Europe (*Ophrys*) and Australia (*Drakonorchis*) loosely resemble female Hymenoptera visually and also produce pheromone-mimicking volatile chemicals and tactile stimulation that target particular bee and wasp species. This mimicry is sufficient to cause males to make repeated attempts to copulate with a succession of flowers, in the process transferring sticky pollen packets.

Myrmecophytes: Arthropods have a variety of mutualistic relationships with plants that do not involve pollination. Some are relatively simple, such as the plant providing a fleshy attachment (elaiosome) to its seeds, to make them more attractive to ants, which will disperse and bury them in the process of harvesting. This is called *myrmecochory*. Many plants collect rainwater in their leaf axils or other structures, providing a specialized habitat for aquatic insects. In return, the insects process the organic matter that falls into these *phytotelmata,* making nutrients more quickly available to the host plant. Insectivorous pitcher plants and their mosquito and fly larvae fall into this category. Still others create tiny shelters (domatia) for predaceous mites, or have glands (extrafloral nectaries) that provide sugar for parasitoid wasps and ants that patrol the plant and disturb or attack plant-feeding insects (Figure 4–11). *Myrmecophytes,* or ant plants, provide shelter, food, or both, to the ants, in return for protection, and have a fairly species-specific and interdependent relationship with them. The best known of these is the bull's horn acacia, a small tree in the Neotropics that provides both food and shelter for one *Pseudomyrmex* ant colony. The ants, including queen and larvae, are housed in large, hollow, twin thorns that are scattered over the branches and twigs. Sugar is provided from extrafloral nectaries at the base of leaf petioles, and protein and fat are derived from Beltian bodies, pellet-like extensions of the leaflets that the ants pick and carry to the thorns for colony distribution. For their part, the ants act as ferocious body guards, biting and stinging both insects and vertebrates that come into contact with the tree. They also prevent competing plants from growing around the base of the tree. An entirely different kind of relationship occurs between *Philidris* ants and bulbous epiphytes (Rubiaceae: *Myrmecodia* and *Hydnophytum*) that grow on small trees in nutrient-poor sandy soils of Southeast Asia. The pseudobulb has rootlets clinging to the host tree and has a single twig of leaves. It is riddled with caverns that house the ants and provide them with cavities for depositing refuse, which consists mainly of remains of the ant's insect prey and of dead ants. The linings of

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Figure 4–11 Two ants drinking nectar from an extrafloral nectary on an *Inga* tree. These ants attack insects that land on nearby leaves.

these cavities appear able to absorb the nitrogenous nutrients from this waste. The ants forage widely and are ineffective in defending either the host tree or the epiphyte against herbivores.

Herbivores: Very few terrestrial or freshwater plants are not fed on by insects. Together, phytophagous insects make up almost half of all insect species. Both tissue feeders and sap suckers may be considered parasites, grazers, or predators, depending on the duration and outcome of the relationship between plant and insect. A single insect that attacks seeds (such as seed bugs, seed weevils) always kills the embryo, and some kinds of stem borers do sufficient damage to the main stalk that an entire plant dies. However, typical grazers (such as leaf, stem, and root eaters with chewing mouthparts) and parasites (such as leaf raspers, leafminers, leaf skeletonizers, and phloem or xylem drinkers with piercing-sucking mouthparts) only weaken the plant or even stimulate new growth, unless they occur in tremendous numbers, as locusts do. Even when gypsy moth caterpillars completely defoliate a tree, new leaves are produced later the same year or following year. Tiny phloem-feeding aphids, ectoparasites equivalent to the blood-feeding lice of mammals, often have an imperceptible impact on the plant's health. Yet heavy infestations of aphids, scale insects, froghoppers, leafhoppers, and various piercing-sucking bugs can cause significant wilting, spotting, browning, fruit drop, and leaf curling, and can precipitate death of the plant. Similarly, endoparasites such as leafminers, stem-borers, and gall-makers can have either marginal effects or serious ones. Stem-borers usually kill the stem in which they develop, thus retarding growth, and bark-boring and wood-boring beetles can weaken trees sufficiently that they die from infection by microbial pathogens. Gall-makers seldom threaten a plant's life, but by applying their secretions they create conspicuous and sometimes disfiguring swellings on the plant. The secretions subvert the plant's own developmental program to produce a distinctive plant structure in which one or more insects can feed and grow to maturity. Most of these are made by gall wasps (most Cynipidae) and gall midges (Diptera: most Cecidomyiidae). Galls also are made by other Hymenoptera (some chalcidoids, braconids, and tenthredinids), other Diptera (some tephritids and agromyzids), Hemiptera (some aphids, psyllids, and coccids), Coleoptera (some weevils, cerambycids, and buprestids), Lepidoptera (some gelechiids), and Acari (some mites).

Plant feeders range widely in host specificity but are conveniently divided into generalists (polyphagous) and specialists (oligophagous and monophagous). In general, the grazers that chew leaves, flowers, and fruit have the broadest tastes (such as Japanese beetles, corn-ear worms, gypsy moths), and the parasites, especially the endoparasites, are the most host specific (such as leafminers, gall-makers). Yet, many species with leaf-chewing larvae have become dedicated to particular kinds of plants containing toxic substances or other defenses that only a specialized insect can overcome (such as monarch butterflies, pipevine swallowtails, zebra butterflies). Herbivores make host choices during the appetitive sequence that leads from a general search to successive and overlapping responses to volatiles, visual appearance, taste, and initial ingestion or oviposition. The behaviors often are elicited by chemical "sign stimuli," kairomones and phagostimulants that are associated only with the family, genus, or species of plant that the insect is adapted to feed on. Specialists have host-detecting equipment and digestive and metabolic systems dedicated to the particular host, giving them a competitive advantage over generalists or allowing them to eat plants from which generalists are excluded altogether. A further advantage is that the host-plant poisons can be incorporated into the insects' bodies, giving them protection from their own predators. Generalists, however, have more food options, making it relatively easy to locate a host plant and providing a large resource base for their populations. Also, their evolutionary fates are not tied to the success of one or a few species of plant.

Plant defenses against phytophagous insects fall into anatomical, chemical, developmental, behavioral, and mutualistic defense categories. Anatomical qualities include (1) visual devices such as unattractive colors and low reflectance, divergent leaf shapes within a genus (making it harder to learn and recognize suitable hosts), and visual mimicry of inedible plants; (2) mechanical and structural devices such as thick and fibrous tissues, spines, hooks, and hairs (trichomes), and sticky sap as a wound response; (3) small seeds that make searching and feeding inefficient. Chemicals include repellents, distasteful substances, natural insecticides, digestive enzyme inhibitors, antimetabolites, and growth regulators (hormone mimics). These properties are produced by various alkaloids, terpenoids, phenolics, proteins, glycosides, and cyanides. Developmental defenses include seed tactics that make seeds and seedlings an unreliable food source: wide dispersal, erratic production, and unpredictable germination or long dormancy. Another developmental defense connects the rate of growth to chemical and structural defenses in one of two strategies. According to the plant apparency hypothesis, plants tend to be either (1) *inapparent* (fast growing, herbaceous, annual, with edible parts available for short periods and with highly toxic substances produced in low concentrations) and are fed on by specialist insects, or (2) *apparent* (slowly growing, woody, perennial, with tough but edible tissues available for long periods and with substances of low toxicity but high concentration, making digestion difficult and slow) and are fed on by generalists. Behavioral defenses consist of diel rhythms of movement or responses to insect attack that make further attack difficult. These include collapsing leaves and petioles and enhanced production of toxic substances both at the site of injury and throughout healthy tissues. Mutualistic defenses are provided by insects that are natural enemies of herbivores. Extrafloral nectaries encourage ants and parasitoid wasps to remain around the plants and attack or infect herbivores. In the case of some myrmecophytes, this arrangement is a deeply involved interdependency (as discussed earlier). Other plants, when injured by phytophagous insects, release volatile compounds that attract parasitoid wasps. These natural enemies inject eggs into the herbivores, and the parasitoids' larvae inflict a slow death.

Insectivorous Plants: A few plants have turned the tables on insects by eating them. These insectivores typically live in nitrogen-poor soils, such as sandy or clay soils and acid bogs, and the prey are biodegraded to release elementary nitrogenous compounds. The plants derive energy from photosynthesis and are not carnivorous heterotrophs. Active traps, such as the Venus flytrap (*Dionaea*), have specialized leaf devices that quickly snap shut to trap small arthropods when triggered by sensitive hairs. In the case of the aquatic bladderwort (*Utricularia*), the prey is sucked into a chamber. Semiactive traps, such as sundews (*Drosera*), flycatchers (*Byblis*), and butterwort (*Pinguicula*), have sticky tentacles or hairs on their leaves to trap the insect, then gradually enfold it to form a digestive cup. Passive traps, such as pitcher plants (*Sarracenia*, *Nepenthes*, and so forth) and cobra lilies (*Darlingtonia*), have leaves modified into vessels of water surrounded by downward-pointing hairs and spines that make escape nearly impossible. Most of these plants have either visually or chemically attractive features, and some bear nectaries that encourage insects to feed near the trap's entrance. Digestion is aided by enzymes, but at least in pitcher plants bacterial degradation of the drowned insect is equally important.

Animal Relationships

Mutualists: Ants have two well-known trophobiotic relationships, one with various stenorrhynchans (Hemiptera) that produce honeydew and one with butterfly caterpillars (Lycaenidae) that produce a glandular secretion. In the case of aphids and scale insects, the basic arrangement is that these plant suckers defecate honeydew (excess phloem sap, rich in sugars and amino acids), and the ants protect them. However, some associations are more involved. Aphids may retain their honeydew until an ant solicits it or have special structures for holding the droplet rather than discharging it. Others have grasping devices to cling to the ants when disturbed, or they may reproduce viviparously throughout the year, so that clones of them are constantly producing large amounts of honeydew. Ants, for their part, solicit honeydew; carry aphid eggs into the ant nest for the winter; select appropriate food plants and carry the aphids to them; apply substances similar to juvenile hormone to the aphids, to prevent them from developing wings; respond to an aphid alarm pheromone by searching for possible enemies; build shelters on the plant to house scale insects; and carry scale insects on nuptial flights in order to establish them in new colonies. Lycaenid caterpillars provide a special substance from a dorsal gland on the abdomen. Ants covet the secretion and provide protection in return. When disturbed, the caterpillars emit a sound that attracts the ants, and within the ant nest the caterpillars are nurtured and protected. Humans and honey bees also have a long history of food-for-care mutualism, although it is not interdependent and is cultural rather than genetic.

Commensals: A large assortment of insects gain by living in close association with other animals, doing little or no harm by their presence. Typically they live in the animal's nest and are known collectively as *inquilines*. In addition to accessing shelter and protection, they eat the host's waste, other inquilines, or the host's food supplies, the latter causing a very slight drain on resources and thus crossing the line into social parasitism. A few species of domestic cockroaches and their human hosts fall into this category. Termites and ants provide an ancient habitat for many specialized inquilines, termed *termitophiles* and *myrmecophiles*, respectively. These fall into three categories: (1) *Synecthrans* are attacked by the hosts but can escape or protect themselves; they scavenge food or waste. (2) *Synoeketes* are ignored by the host because they move quickly or do not appear foreign; they generally scavenge food or waste but also sometimes kill and eat host immatures. (3) *Symphiles* are accepted by the host as members of the colony; they may be fed, carried, and groomed by the host. Symphiles share various characteristics that suit them to this role: They secrete appeasement substances that the hosts find attractive and palatable; they have chemical, tactile, or visual resemblances to the host (Wasmannian mimicry), or they have a sheltering carapace that prevents hosts from contacting vulnerable parts; they exhibit morphological regression, including flightlessness and reduction or loss of eyes and appendages; and they use the chemical and behavioral communication systems of the host, including alarm, attraction, mutual grooming, solicitation of food, and trail following.

Parasites: Arthropods parasitize a wide variety of animals, including other arthropods. Typical ectoparasites suck the hemolymph or blood of their hosts, either remaining on the host continuously (that is, symbiotically) (such as lice, host fleas, and some mites) or visiting it only periodically (such as kissing bugs, nest fleas, mosquitoes, and horse flies) (Figure 4–12). The closely adapted ones have a number of characteristics suited to life on another animal, including the reduction or elimination of wings, legs, and eyes; special clinging and attachment devices; and body flattening. Periodic blood feeders share behavioral and physiological features, including special receptors for locating hosts, sneakiness, painless biting, antihemostatic and anticoagulant properties of the saliva, and presence of mutualistic bacteria (discussed earlier). Endoparasites, such as strepsipterans parasitic in insects and scabies mites or bot flies in vertebrate animals, also have distinctive traits that allow them to find, enter, and live within the host. The so-called human bot fly, or tórsalo, whose larva develops in the skin of mammals and large birds, is a large, free-living adult. To avoid disturbing its host during oviposition, it lays its eggs on mosquitoes or small domestic flies. When these carriers land on the skin, the larvae immediately hatch and burrow in. Endoparasites obtain oxygen by tapping into the host's tracheal system (in the case of insect hosts) or maintaining a hole in the host's skin where the spiracles can be exposed to air. Stomach bot-fly larvae of horses circumvent this necessity by using hemoglobin cells to store oxygen that comes as occasional air bubbles with the horse's food. As with plant feeders, animal parasites find their hosts in a series of oriented maneuvers, starting with a general search and ending in landing, probing, and feeding. Periodic blood feeders use chemical stimuli (kairomones such as fatty acids from skin bacteria and carbon dioxide from breath) to locate mammals at a distance, to which are added visual stimuli when the host is closer, heat and humidity at very close range, and skin chemicals on contact. Host-specific sign stimuli, perceived by the parasite during these steps, are critical in the decision to continue the attack or desist. Parasites tend to be relatively host specific, the periodic ones least so, the continuously ectoparasitic species much more so, and the endoparasites most of all.

Important variations on the parasite theme are *parasitoids* (often referred to simply as *parasites*), whose larvae first are parasites on or inside an appar-

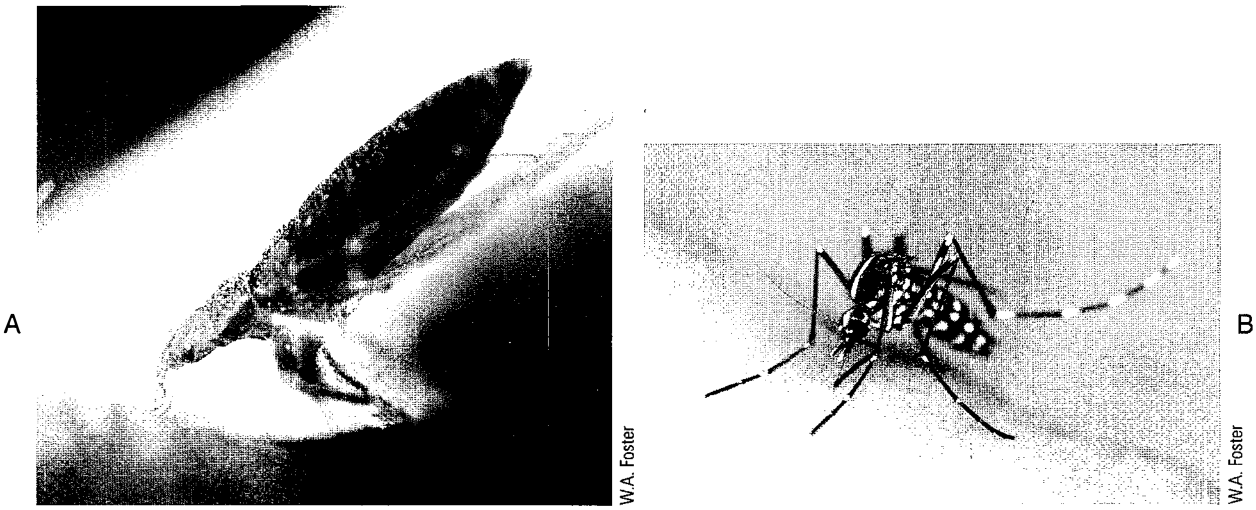

Figure 4–12 Periodic blood feeders of vertebrate animals. A, Human bed bug feeding. This species (*Cimex lectularius*) lives within human habitations. All members of the family Cimicidae are wingless blood feeders throughout life and most live in the roosts and nests of bats and birds. B, Asian tiger mosquito feeding. This species, *Aedes albopictus* (Skuse), often lives near human dwellings, but not in them, and occurs mainly in rural or wooded areas. All adult members of the family Culicidae have wings, and the females of most species feed on blood. Their larvae are mostly free-living detritivores.

ently healthy insect host but gradually eat more and more of the host's internal organs until it becomes moribund and dies. Essentially the same thing happens when a solitary hunting wasp paralyzes its prey, uses it to provision a nest, and lays an egg on it, although in that case the host immediately ceases to function normally. Parasitoid insects typically are small and lay their egg(s) in the host where they find it. They tend to be very host and stage specific, developing, for example, only in the eggs of a particular moth, or only in the parasitoids that develop in those moth eggs (that is, hyperparasitoids). The latter are exceedingly small. But as a group parasitoids attack a wide variety of insects, including many pests, and therefore are useful in biological control. Females may lay many eggs in a single host, so that a large family develops in it. Among some of the parasitic hymenopterans (e.g., Braconidae) are females that lay only a single egg in the host, but the egg undergoes polyembryony, resulting in numerous larvae. Parasitoids may pupate within the host if it dries out by the time they are mature. Typically they exit the host and pupate on its cuticle or nearby (Figure 4–13). Parasitoids are most common among Diptera and Hymenoptera. Tachinids are the most important fly parasitoids; others include sarcophagids, pyrgotids, pipunculids, acrocerids, and bombyliids. Hymenopteran parasitoids include many hundreds of species in the Ichneumonoidea, Chalcidoidea, Proctotrupoidea, Platygastroidea Chrysidoidea, and Vespoidea. Rhipiphorid beetles, which undergo hypermetamorphosis, are parasitoids during the second phase of their larval lives. The Strepsiptera also are hypermetamorphic but do not kill their hosts. Instead, they often sterilize them or turn them into intersexes, so in one sense they are parasitoids, because they can kill the host's reproductive potential.

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Figure 4–13 Tobacco hornworm, *Manduca sexta* (L.) (Sphingidae), in final stage of parasitization by the parasitoid *Cotesia* (Braconidae). The larvae have completed development within the caterpillar, then exited to spin cocoons in which they pupate. Some have already emerged as adults, and some cocoons have dropped off, leaving black spots at the point where the larva had burrowed out. This brood of parasitoids typically results from a single egg that has been inserted into the caterpillar and undergone polyembryony, creating a family of identical offspring.

Predators: Predatory arthropods include most orders of Arachnida, all Odonata and Mantodea, and nearly all Neuroptera. A great many Hemiptera, Coleoptera, and Diptera also are predators. Like the parasitoids, they prey on a variety of small animals, but mostly other arthropods, so they are said to be *entomophagous*. Predators with chewing mouthparts eat most or all of their prey; those with piercing-sucking mouthparts pierce the prey's cuticle, inject a lytic saliva to liquefy the tissues, and suck out the resulting soup (Figure 4–14). Like plant feeders and animal parasites, there are generalists and specialists, but in this case the reasons for specialization are less often physiological and have more to do with habitats, competition, methods of hunting, and special techniques of prey capture. Most species of dragonflies, assassin bugs, mantids, and many kinds of army ants and driver ants eat diverse types of prey that occur within the habitats they frequent. By contrast, different genera of digger wasps (Sphecidae: Sphecinae) specialize in spiders, cockroaches, grasshoppers, katydids, tree crickets, true crickets, plant-dwelling caterpillars, or soil-dwelling caterpillars. There are two basic approaches to prey capture: (1) *Hunting* is most efficient if the prey are sedentary, slow moving, or are most abundant in locations where a predator cannot wait (for example, in mid-air). The predator moves though likely habitats, increasing its chances of encountering the prey. (2) *Awaiting and stalking* work well when the prey are mobile and likely to pass by. The predator remains in one place until prey is detected, then stalks it and/or grasps it.

Equipment that assists predatory arthropods in seizing prey include raptorial fore legs, often with spines or sticky setae, and raptorial mouthparts, such as the extensible labium of odonate naiads and the long, curved mandibles of diving beetle larvae and tiger beetles. Insects with a venomous bite or sting (spiders, scorpions, antlions, female hymenopterans) can paralyze the prey with a single, well-placed injection, making them easier to handle. Beaded lacewing larvae (Berothidae) subdue their prey with a chemical ejected from the anus. Hunting wasps do their hunting primarily to provision nests for their larvae, and the paralyzed prey forms a living meal when the larva is ready to eat. Some of the sit-and-wait predators have devices that improve their catch: traps, lures, or a

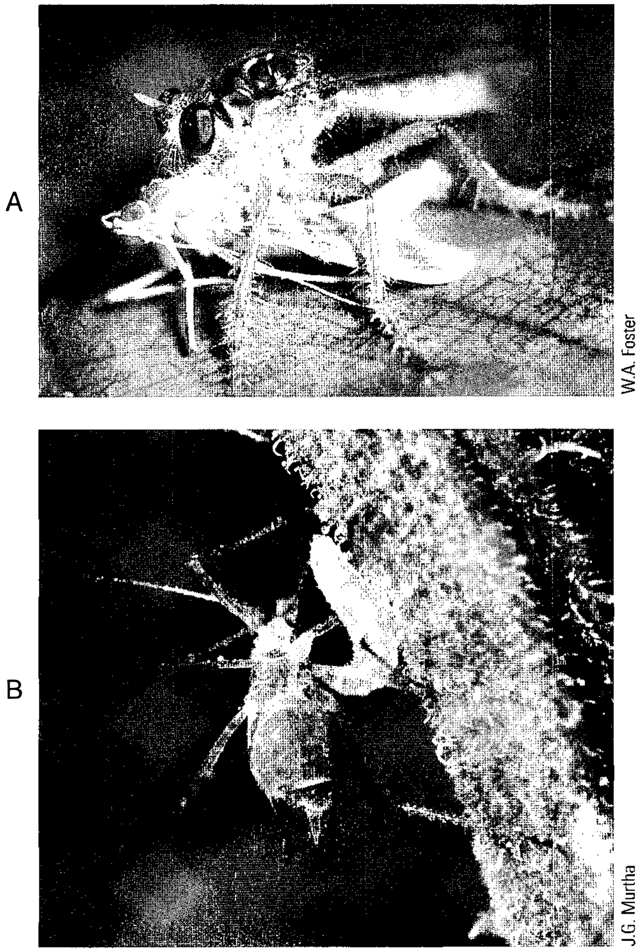

Figure 4–14 A, Robber fly (Asilidae) feeding on moth. Robber flies typically await prey from perches, then fly out to seize them in mid-air. The proboscis is inserted into the prey; lytic saliva is injected, and then digested tissues are withdrawn as liquid. The proboscis also can be used as a defensive weapon. **B**, Flower fly larva (Syrphidae) feeding on an aphid. Because aphids tend to be sedentary, they are easily seized by predators, including those that have smaller bodies.

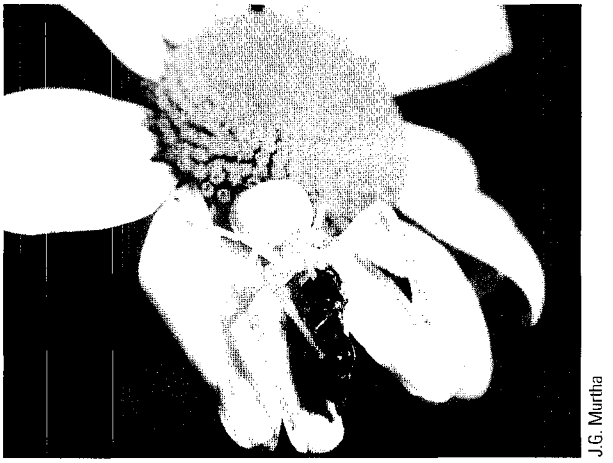

Figure 4–15 White crab spider (Thomisidae) feeding on a syrphid fly it has captured at the flower. Predators with this ambush tactic often blend well with the flowers on which they wait, either to avoid detection by potential prey or to avoid detection by their own predators.

combination of the two. Traps include the sticky aerial webs of spiders, the aquatic nets of some caddisfly larvae, and the sand pits of antlion (Myrmeleontidae) and wormlion (Vermileonidae) larvae. Lures include flowers, which attract insect prey to within striking distance of predators that wait on or behind the flower. Crab spiders and ambush bugs apply this technique. Often they are the same color as the flower where they wait (Figure 4–15), and some mantids look like flowers themselves. It is not clear if this concealment or disguise facilitates prey capture or prevents predation by the predators' own enemies. Insect-generated lures include bright lights (Waitomo worms, larvae of mycetophilid larvae that live in caves in New Zealand and attract insects to their sticky-stranded webs), flashing lights (female *Photuris* fireflies that attract *Photinus* males to their deaths by mimicking the answering signal of a receptive *Photinus* female), and attractive chemicals (bolas spiders that mimic female moths by releasing moth sex pheromones and snaring male moths that come within range of their sticky bolas). The last two examples exhibit the tactic known as *aggressive mimicry*.

Arthropods are prey for many vertebrate animals. They form much of the diet of freshwater fish, amphibians, reptiles (notably lizards and small snakes), many groups of birds (such as flycatchers, bee eaters, warblers, creepers, woodpeckers), and some mammals (notably shrews, small bats, and anteaters). Even vertebrates that do not specialize in arthropods make them an important part of the diet during the breeding season (for example, hummingbirds, squirrel monkeys) or include them as a minor constituent of their omnivorous diets (for example, field mice, chimpanzees, humans). Predation pressure on arthropod populations has led to a spectacular array of protective measures directed primarily against vertebrate predators. These may be classified as follows: (1) *Defense and offense* discourage an attack by resisting, threatening,

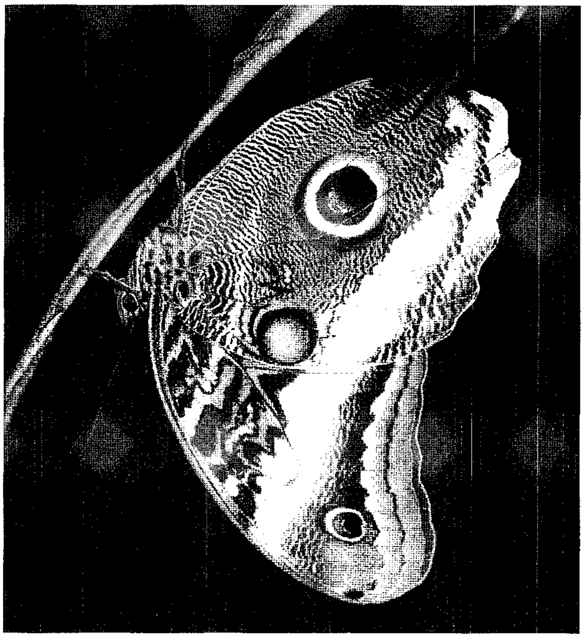
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Figure 4–16 Eye spot on owl butterfly *Caligo* (Satyridae: Brassolinae). Eye spots occur on many kinds of insects. Experiments demonstrate that vertebrate animals are frightened by them, probably because of their resemblance to the eyes of large predators, such as owls and cats.

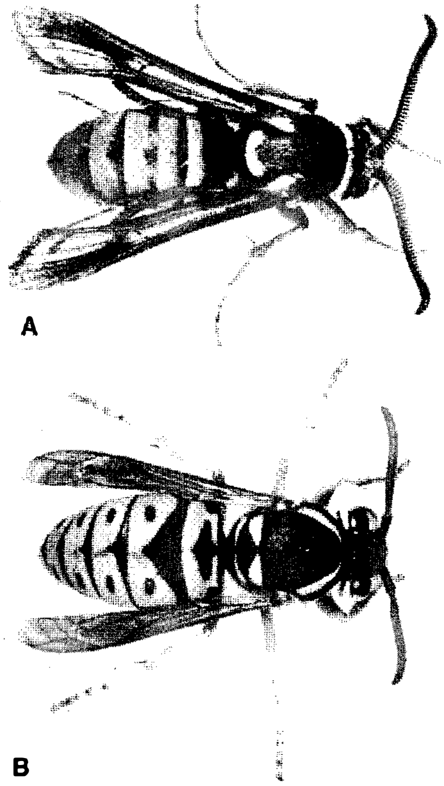

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Figure 4–17 Mimicry of a yellow jacket (B) by a clearwing moth (*Parathene* sp.)(A).

or injuring a predator. The devices may be mechanical, chemical, or visual, may involve mutualistic defenders, such as pugnacious ants (discussed earlier), and may be used actively, passively, or both. Active mechanical defenses include biting, spiking, stinging, and frightening sounds; passive defenses include spines, hairiness, and thick, hard cuticles. Chemically defended insects deploy allomones, including noxious, painful, and poisonous substances that are actively ejected from the body or injected by sting into the victim's body, or are deployed passively within the insect or available in needlelike spines that penetrate the predator on contact. Visual defenses include frightening or threatening appearance (sudden movements, startle displays, flash colors, eyespot exposure, predator simulation = defensive mimicry) (Figure 4–16), aposematism (warning colors, lights, and sounds that are combined with chemical or mechanical defenses that the predator learns), and Müllerian mimicry (warning signals shared among several distasteful species, which serve as both models and mimics of each other, providing mutual protection). Aposematic insects typically use bold colors, such as red, orange, yellow, or white, presented as stripes, spots, bars, and rings on a contrasting dark background. These patterns are easily learned and easily seen. The insects enhance the patterns' effectiveness by behaving ostentatiously (for example, being exposed openly, walking and flying slowly, waving conspicuous body parts) and forming aggregations. Familiar Müllerian mimics are the warning-colored and aggressive vespid wasps, which share yellow-and-black markings. Tropical Müllerian "rings" include a host of slow-flying, long-winged butterflies and moths that share a common orange-yellow-black color pattern and behavior. Some members of such rings are not distasteful and therefore are Batesian, rather than Müllerian, mimics. (2) *Disguise* involves appearing to be something else, so the attack is not initiated. This includes the following: (a) *Batesian mimicry,* in which an unprotected mimic resembles a distasteful species—the model—with which the predator has had an unpleasant experience. Batesian mimic-model systems are ubiquitous, most commonly seen among various flies, beetles, and moths (Figure 4–17) that mimic wasps

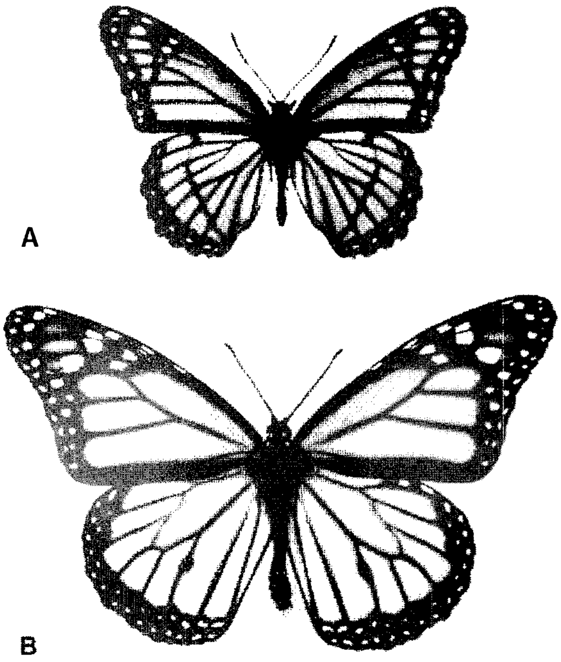

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Figure 4–18 An example of mimicry in butterflies. A, The viceroy, *Basilarchia archippus* (Cramer); B, The monarch, *Danaus plexippus* (L.).

and bees. This tactic includes insects whose body parts resemble a separate insect. A widely cited North American Batesian mimic is the viceroy (Figure 4–18), a usually edible butterfly that closely resembles the monarch, a butterfly whose body contains poisonous cardiac glycosides derived from milkweed on which the larva feeds. A variation on Batesian mimicry is the resemblance of an edible mimic to a model that the predator learns is difficult to catch. Thus, some weevils closely resemble sarcophagid flies. (b) *Wasmannian mimicry*, in which symphiles resemble their carnivorous, defensive social hosts (discussed earlier) and thereby prevent host attack. Symphiles that travel outside the nest with their hosts frequently function as Batesian mimics, too. (c) In *object resemblance*, the insect looks like an inanimate and inedible object, such as a rock, stick, leaf (Figure 4–19), or feces (Figure 4–20). (d) In *thanatosis*, the insect feigns death. (3) In *concealment*, the insect seems not to be there. This approach includes background resemblance, countershading (= obliterative shading: body appears flat, rather than solid and three-dimensional), shadow elimination (body appears joined to substrate), disruptive coloration (body outline is obliterated), natural camouflage (body covered with natural materials, such as tree bark, living lichens, the remains of an insect's prey, or its own feces), and hiding in an unexposed place; insects can hide under physical objects or in nests or cases of their own construction. Open concealment works best when the insect remains motionless.

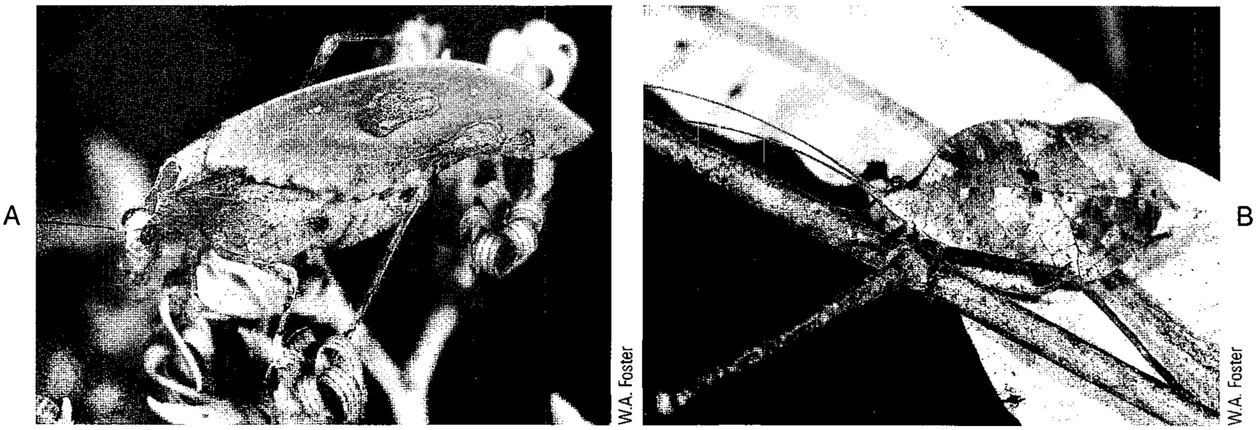

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Figure 4–19 Katydids (Tettigoniidae) that resemble (A) diseased or dying leaf, (B) completely dead leaf. Details of this disguise include designs that suggest the presence of a leaf midrib and methods for concealing the presence of legs.

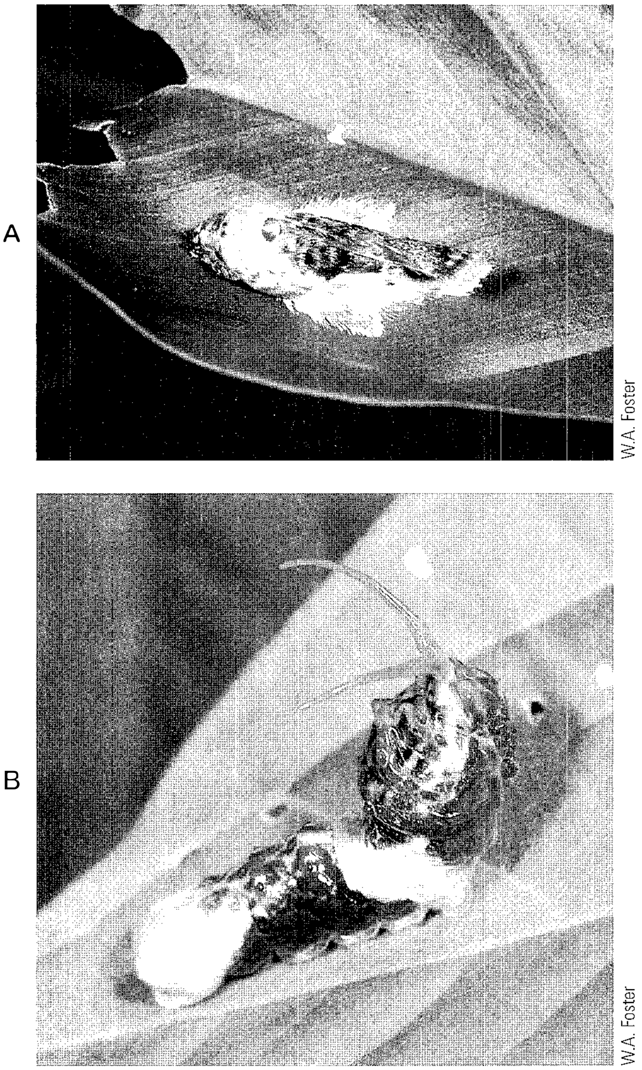


Figure 4–20 Bird-feces resemblance: Insects using this disguise depend on a composite of brown and white colors, typical of bird feces. A, Moth openly exposed on a leaf at rest, resembling bird feces. The elongate scales extend laterally, giving the impression of splatter. B, Swallowtail butterfly larva. Its glossy cuticle gives the impression of wet bird feces. Its second line of protection, when disturbed, is to extend the two-pronged glandular horn (the osmeterium) behind its head, which releases a noxious vapor.

(4) *Escape and evasion* involve being hard to capture, so the predator cannot complete the attack. This method occurs in two forms: (a) In *fleeing* the predator cannot maintain pursuit or achieve capture, such as fast escape (by running, jumping, swimming, flying, dropping), evasive maneuvers, and detachable body parts. (b) In *disorientation* various deceptive structures or behaviors cause the predator to desist from attack or fail to complete the attack. This includes *deflection*, the use of conspicuous marks, a false head, and autotomy (dropping a body part), to direct the predator's attention toward expendable items while the prey escapes in an unanticipated direction; and *confusion*, the use of strange shapes and movements (predator does not recognize it as prey) and swarming (predator has difficulty concentrating on one individual).

There are two things to keep in mind about the preceding antipredator-device categories: First, not all cases fall neatly into a single category, but rather combine aspects of two or more tactics. Second, many specific instances of disguise, concealment, warning, and so on have been inferred from their appearance to the human eye and have yet to be tested experimentally. Yet, so far, all carefully reasoned inferences have been confirmed by experimentation.

Detritivores

A large proportion of arthropod species feed on dead and decaying plants and animals, recycling them into living biomass. These saprophagous arthropods occur in many orders but are found chiefly in the Acari, Blattodea, Isoptera, Coleoptera, and Diptera. They all have chewing, rasping, or chelate mouthparts. Most specialize either in plant or animal materials, partly because ovipositing adults locate them by very different means but also because different digestive mechanisms are employed. Technically, most detritivores do not feed exclusively on dead material itself but feed instead on a mixture that includes bacteria, fungi, nematodes, and other minute organisms that occur with dead tissue and share in its breakdown. The detritus community also includes predators and parasites that feed on the detritivores. What makes saprophagous insects especially important, ecologically, is that they are relatively large and mobile, dispersing large amounts of detritus by working it into the soil, carrying it to scattered locations, or completing their life cycles in it so that the next generation flies away.

Plant detritivores live chiefly in the immediate vicinity of standing crops of plants, such as forests, grasslands, and ponds, where the dead material accumulates on the ground or in aquatic sediments. A large part of the soil microfauna of the world consists of various mites, millipedes, springtails, and beetles that feed on finely divided plant material and its associated microorganisms. More obvious on the forest floor are fallen leaves, branches, and tree trunks, which also support a diversity of arthropods and hasten their conversion into soil. Even recently killed trees that are still standing attract specialists whose larvae develop within the wood. By processing the larger components of plants, large arthropods make plant matter more readily available to microscopic arthropods, to microbes, and ultimately to the root systems of living plants as mineral nutrients.

Animal detritivores form a much smaller part of most communities, because much less animal material is available for degradation. Some arthropods, such as adult scorpionflies, specialize in the dead bodies of other arthropods, but the most obvious ones process the dead bodies of medium-sized and large vertebrates. In its early stages of decay, a carcass is so rich in organic nutrients and is so easily digested, that sarcophagous (= flesh-eating or carrion-feeding) insects engage in intense scramble competition. The most quick and efficient of these are the blow flies and flesh flies, which in warm, humid weather can reduce a large corpse to a skeleton in a few days. Gravid females start laying eggs in an animal's orifices within an hour of its death, and the eggs hatch in less than a day (or are deposited as ready-to-feed larvae, in the case of flesh flies). When the hundreds or thousands of fly larvae (maggots) have matured, they crawl away and pupate underground nearby. Other carrion feeders specialize in small birds and rodents. A mated pair of burying beetles lowers the carcass into the ground and converts into an edible nest for its young (as discussed earlier).

Dung-feeding (coprophagous) arthropods are, ecologically, either plant or animal detritivores, depending on the diet of the animal producing the feces. Insects tend to specialize in the dung of kinds of different kinds of animals, because the size and consistency of the dung pile determines its shape and volume and therefore how quickly it will dry out. Dung beetles (Scarabaeidae), as a group, are able to use the greatest variation in dung-pile sizes, because some species develop within the dung in situ, but others quickly gather the dung into packets or balls and lower it into tunnels beneath the pile or roll it away, to provision their underground nests. Yet different dung beetle species focus on dung from herbivorous mammals of different sizes. Larval development of flies occurs within the dung pile itself, so relatively large dung piles, such as the "cow pats" produced by large ungulates, form the best breeding medium. One important consequence of this situation was that introducing cattle to Australia also introduced a huge source of dung, which the native kangaroo-dung beetles could not handle, but which was ideal for bush flies and buffalo flies. Importation of African dung beetles that disintegrate cow pats have helped bring pest fly populations under control.

Animal carcasses and dung piles are "fugitive habitats," environments with resources that quickly dissipate. During the period of utility, they are invaded by successive but overlapping waves of insects that deal effectively with certain stages in the degradation and drying process and with each other. A cow pat in North America often is invaded first by horn flies and face flies, whose females oviposit on it immediately after the feces drop to the ground. Yellow dung flies, sepsids, and ulidiid flies come, then leave, at various stages as it cools and a crust forms. These are followed by scarab and hydrophilid beetles, and by staphylinid beetles that either feed on the eggs of other insects or parasitize developing fly larvae. Soldier flies show up still later. By the time the cowpat is stiff and only moist in the middle, it is occupied primarily by the larvae and pupae of slow-growing fly and scarab-beetle larvae, each developing in zones of the cow pat that differ in physical characteristics (crust, center, base). Arthropod succession in carcasses follows a similar pattern, typically with blow flies appearing first, beetles later. In late stages of decay, the carcass community may consist mainly of dermestid beetles and moths that eat dried skin and ligaments. The exact species composition and rate of change depend not only on the geographic locality but also on the exact habitat (carcasses transform very differently in sun and shade), weather, and season. Knowledge of the pattern and speed of faunal succession in a carcass can be critical to forensic investigators. From data on the arthropod species and their stages in a corpse when it is discovered, it is possible to estimate the postmortem interval and thus the time of death.

Insect Impact in Biotic Communities and Ecosystems

Insect Diversity

Insects are vitally important members of biotic communities for two reasons: There are so many of them, and there are so many different kinds. The average abundance of any one species is simply a function of how small it is, how large its resource base is, and how many enemies exploit it. But insects are unusual among organisms in their abundance of species. According to conventional ecological theory, each species occupies a unique niche, a unique way of living that it performs better than any other species and that is defined by where it lives and what it consumes. In some communities insect species are so tightly packed that they have extensively overlapping niches, resulting in

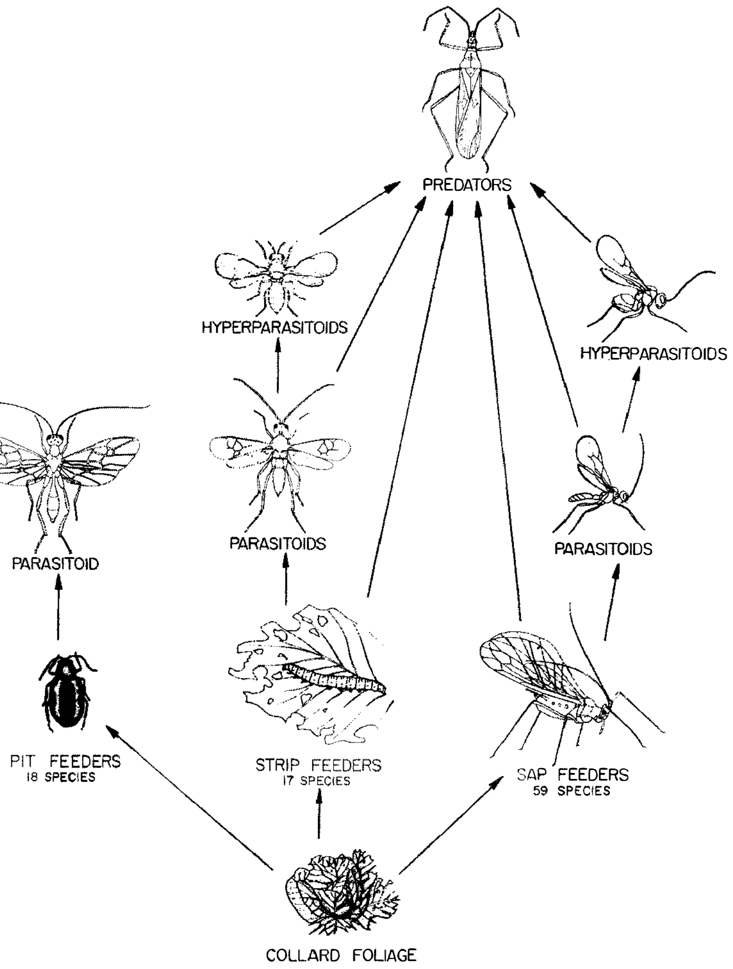


Figure 4–21 Food web on a single plant, illustrating the presence of three guilds of plant-feeding insects: 18 species of pit feeders, 17 species of strip feeders, and 59 species of sap feeders. The parasitoids and predators of these insects, not numbered, also form guilds.

competition, but partitioning and environmental instability prevent the exclusion of one competitor by another. Thus we find many insect guilds, groups of insect species that use the same food source but do so in slightly different ways (Figure 4–21). The fact that over half of all described species of organisms, and about three quarters of all animal species, are insects suggests they are exceptional in their ability to assume a myriad of unique lifestyles.

There appear to be four interconnected reasons for this diversity, all directly or indirectly resulting in a high speciation-to-extinction ratio: (1) *Exoskeleton:* This is the strongest and most efficient skeleton for small-bodied animals. In addition to giving body support, external protection, and opportunities for evolving a wide variety of hard tools for handling food and other materials, it provides leverage for long appendages, allowing elevated body support and quick movements, and it offers resistance to desiccation. These features allowed arthropods to become the first animals to invade land, along with vascular plants, so a vast variety of potential niches were available to them, and they could diversify along with the plants. (2) *Small size*: More niches are available to small-bodied animals, because many kinds of food and space are available only in small quantities and limited sizes. Small animals also have shorter generation times, allowing rapid evolution and adaptation to new conditions. And small animals have a large surface-to-volume ratio, which has beneficial consequences: (a) proximity of organs to each other, which allows use of simple circulatory and respiratory systems; (b) greater muscle strength in relation to size, which allows thinner limbs; and (c) greater air resistance, which allows greater wing and body loft, facilitating airborne dispersal and evolution of powered flight. However, a large surface area is disadvantageous because desiccation and heat loss are more rapid. (3) *Wings:* The greater mobility provided by flight allows animals to exploit widely scattered resources, which form distinct niches. Furthermore, it allows them to colonize new areas rapidly, reducing the likelihood of extinction and providing opportunities for genetic isolation and species formation. (4) *Complete metamorphosis:* Transformation of the body from one kind of animal to another has the following consequences: (a) a temporary resource that is only part of a unique niche can be exploited without having to sustain all active stages; (b) more unique niches are available, because the "compound niche" of the two different active forms (larva and adult) is, as a whole, another niche, reducing competition with overlapping species and avoiding competitive exclusion even by species that occupy only one niche or the other; (c) individuals escape from natural enemies by disappearing from one of the microhabitats before enemies become too numerous; (d) specialization in either growth and storage (the larva) or dispersal and reproduction (the adult) results in increased efficiency of each stage. The fact that most insect species occur in orders with complete metamorphosis suggests that this feature is exceptionally important.

Population Size and Its Control

The numbers of individuals in an insect population is determined first by the size of the entire community in which they can exist, their biotope. Beyond that, their density is controlled by an array of exogenous and endogenous factors affecting reproduction, death, and migration rates. Exogenous factors are principally food, space, natural enemies (predators, parasites, pathogens), and weather. The first three vary in their intensity according to how dense the population is, and are termed *density-dependent* factors, responsible for regulating the density within somewhat narrow bounds around the species' *equilibrium density*. Weather-related factors, in contrast, usually are *density-independent*, having an effect proportional to insect numbers. The latter are responsible for wide and erratic population fluctuations. The endogenous factors are all density dependent, including changes in disease-inducing stress levels, social interactions, emigration rates, and gene pool composition. The density-dependent/independent distinction is a useful concept, but insect populations often are controlled by a complex interplay of weather-related biotic factors, so that equilibrium densities are superimposed on erratic or seasonal changes caused by changing physical conditions. In other words, an insect may have several equilibrium densities, depending on the weather, and if the effects of weather change often enough, population regulation is almost completely obscured. Some insect populations may never reach the point where reduced resources and increasing predation prevent further population growth. In others, fluctuations are caused by density-dependent factors that have effects extending long beyond the immediate causes (for example, desert locusts, as mentioned earlier) or are the result of environmental feedback that works over time scales of many years (many forest Lepidoptera). Therefore, an intimate knowledge of natural population control may be necessary before insect outbreaks can be predicted with any reliability.

Artificial Control: The principles that determine population density in nature can be applied by humans to the judicious control of insect pests. Pest control is not appropriate, economically, unless pests are dense enough to reduce the value of some product or resource more than it costs to prevent that reduction. The breakeven point, the pest density at which the gain in value from control is equal to the cost of that control, is the *economic injury level,* or *EIL*. For insects that are largely density dependent, the relationship between the EIL and the equilibrium density determines whether measures should ever be taken against them. Some pests cause relatively minor damage to crops, livestock, or human health, rarely exceeding their EILs, because their equilibrium densities are low, thanks to natural enemies or restricted breeding sites. Others may cause extensive damage but still rarely exceed their EILs. This occurs if control is very expensive, the product has a low value, or it is tolerant to high damage so the economic loss is small. However, when pests surpass a certain lower level (the *economic threshold*) indicating that they soon will exceed the EIL, control measures should be implemented immediately in order to take effect by the time the EIL is reached. Aside from environmental concerns, the decision to control pests in agricultural systems has an exclusively economic basis. The decision to control insects of medical importance is complicated by the need to consider not only losses in human

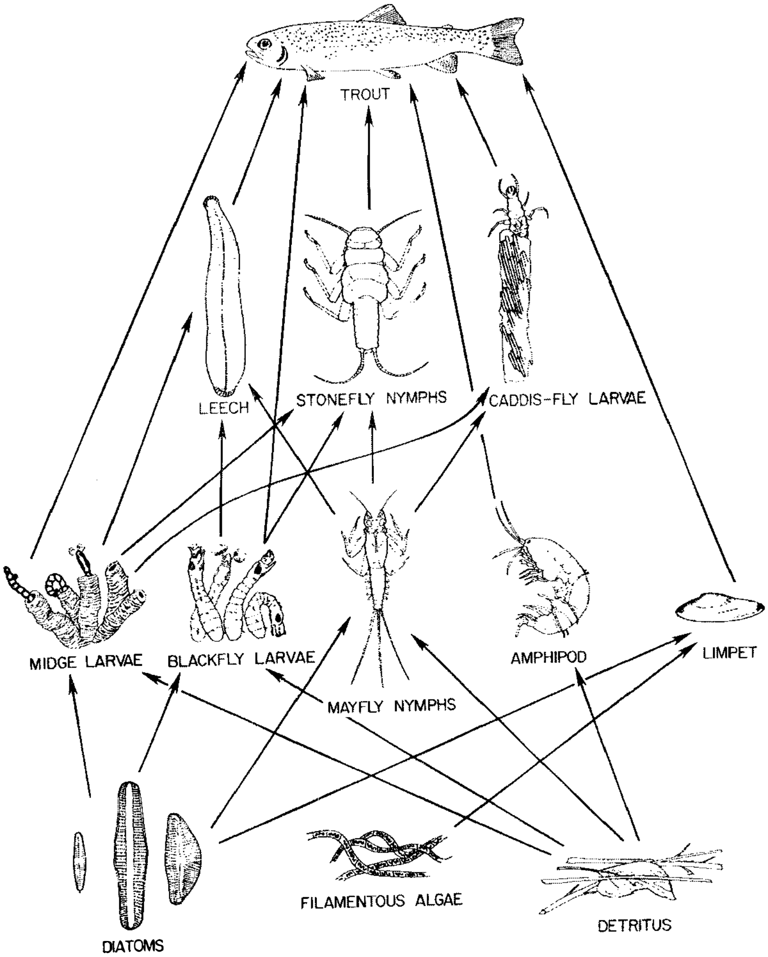


Figure 4–22 Simple freshwater aquatic food web, showing the pivotal roles of insects at the primary- and secondary-consumer trophic levels.

productivity and costs of treatment, but also the amount of suffering caused. A knowledge of what determines the natural equilibrium density may be crucial to effective time management. For example, the application of pesticides may temporarily eliminate natural enemies of the pest, not just the pest, causing its rapid rebound and *biotic release*. In this reaction, the pest density soars until it finds a new, higher equilibrium position, causing more damage and requiring more frequent application of insecticides. This situation, which is costly and can lead to insecticide resistance more quickly, is known as the "pesticide treadmill." For both density-independent and density-dependent pests, knowing how weather-related factors and biotic factors combine to determine population growth and depression help entomologists anticipate conditions when the EIL will be exceeded. The ideal goal is to find low-impact ways to alter a pest's environment so that the EIL is never reached and insecticides are unnecessary.

Insect Roles in Food Chains and Webs

Insects and other arthropods are major constituents of trophic pyramids because of the sheer mass of numbers in populations of each species at all consumer levels. In every case studied, insects eat and incorporate far more energy than vertebrate animals in the same communities. In fields in North America, more than three quarters of the energy flow from plants passes through populations of a few species of Orthoptera, dwarfing the importance of birds and mice. In terms of living biomass, just the ants of the world, a single family consisting of about 11,000 species, weigh as much as the 6 billion humans of the world. In the Amazon rain forest, ants and termites make up about one third of the biomass of all animals, from mites to tapirs, and the dry weight of ants there is four times as great as the dry weight of all land vertebrates combined. Even at the very tops of the food chains, which generally are perceived as being occupied by such carnivores as eagles and lions, the ectoparasitic lice, fleas, biting midges, and skin mites feed on these so-called top predators. In addition, arthropods are pivotal in a myriad of intersections within food webs (Figure 4–22) because of their diversity, as reflected in the number of species in every terrestrial and freshwater community. Without arthropods in the picture, communities most likely would consist of fewer trophic levels, with drastically reduced trophic links among the remaining organisms.

References

Alcock, J. 1979. Animal Behavior: An Evolutionary Approach, ed. 2. Sunderland, MA: Sinauer Associates, 532 pp.

Andersson, M. 1994. Sexual Selection. Princeton, NJ: Princeton University Press, 599 pp.

Baerends, G. P. 1976. The functional organization of behaviour. Anim. Behav. 24: 726–738.

Barth, F. G. 1991. Insects and Flowers: The Biology of a Partnership. Princeton, NJ: Princeton University Press, 408 pp.

Barton Browne, L. 1974. Experimental Analysis of Insect Behaviour. New York: Springer, 366 pp.

Bell, W. J., and R. T. Cardé (Eds.). 1984. Chemical Ecology of Insects. Sunderland, MA.: Sinauer Associates, 524 pp.

Cardé, R. T., and W. J. Bell (Eds.). 1995. Chemical Ecology of Insects 2. New York: Chapman & Hall, 433 pp.

Chapman, R. F. 1998. The Insects: Structure and Function, 4th ed. New York: Cambridge University Press, 770 pp.

Choe, J. C., and B. J. Crespi (Eds.). 1997. Evolution of Social Behavior in Insects and Arachnids. New York: Cambridge University Press, 541 pp.

Choe, J. C., and B. J. Crespi (Eds.). 1997. Mating Systems in Insects and Arachnids. New York: Cambridge University Press, 387 pp.

Crozier, R. H., and P. Pamilo. 1996. Evolution of Social Insect Colonies: Sex Allocation and Kin Selection. New York: Oxford University Press, 306 pp.

Dawkins, R. 1976. Heirarchical organization: A candidate principle for ethology. In P. P. G. Bateson and R. A. Hinde (Eds.), Growing Points in Ethology, New York: Cambridge University Press, pp. 7–54.

Dingle, H. (Ed.). 1978. Evolution of Insect Migration and Diapause. New York: Springer, 284 pp.

Dingle, H. 1996. Migration. The Biology of Life on the Move. New York: Oxford University Press, 474 pp.

Dyer, F. C. 2002. The biology of the dance language. Annu. Rev. Entomol. 47: 917–949.

Eberhard, W. G. 1996. Female Control. Sexual Selection by Cryptic Female Choice. Princeton, NJ: Princeton University Press, 501 pp.

Evans, D. L., and J. O. Schmidt (Eds.). 1990. Insect Defenses. Albany: State University New York Press, 482 pp.

Fraenkel, G. S., and D. L. Gunn. 1961. The Orientation of Animals. New York: Dover, 376 pp.

Frank, S. A. 1998. Foundations of Social Evolution. Princeton, NJ: Princeton University Press, 268 pp.

Frisch, K. von. 1967. The Dance Language and Orientation of Bees. Cambridge, MA: Belknap Press, 566 pp.

Gadagkar, R. 1991. *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent founding *Ropalidia*. In K. G. Ross and R. W. Matthews (Eds.), The Social Biology of Wasps, pp. 149–100. Ithaca, NY: Cornell University Press.

Holldobler, B., and E. O. Wilson. 1990. The Ants. Cambridge, MA: Belknap/Harvard University Press, 732 pp.

Houston, A. I., and J. M. McNamara. 1999. Models of Adaptive Behavior: An Approach Based on State. Cambridge, UK: Cambridge University Press, 378 pp.

Ito, Y. 1993. Behaviour and Social Evolution of Wasps. New York: Oxford University Press, 159 pp.

Lloyd, J. E. 1983. Bioluminescence and communication in insects. Annu. Rev. Entomol. 28: 131–160.

Mangel, M., and C. W. Clark. 1988. Dynamic Modeling in Behavioral Ecology. Princeton, NJ: Princeton University Press, 308 pp.

Matthews, R. W., and J. R. Matthews. 1978. Insect Behavior. New York: Wiley, 507 pp.

McFarland, D. J. (Ed.) 1984. Motivational Control Systems Analysis. New York: Academic Press, 522 pp.

Michener, C. D. 1974. The Social Behavior of Bees: A Comparative Study. Cambridge, MA: Belknap/Harvard University Press, 404 pp.

Mittelstaedt, H. 1962. Control systems of orientation in insects. Annu. Rev. Entomol. 7: 177–198.

Papaj, D. R., and A. C. Lewis (Eds.). 1993. Insect Learning. Ecological and Evolutionary Perspectives. New York: Chapman & Hall, 398 pp.

Price, P. W. 1997. Insect Ecology. New York: Wiley, 874 pp.

Real, L. A. (Ed.). 1994. Behavioral Mechanisms in Evolutionary Biology. Chicago: University of Chicago Press, 469 pp.

Roitberg, B. D., and M. B. Isman (Eds.). 1992. Insect Chemical Ecology. An Evolutionary Approach. New York: Chapman & Hall, 359 pp.

Thornhill, R., and J. Alcock. 1983. The Evolution of Insect Mating Systems. Cambridge, MA: Harvard University Press, 547 pp.

Tinbergen, N. 1951. The Study of Instinct. London: Oxford University Press, 228 pp.

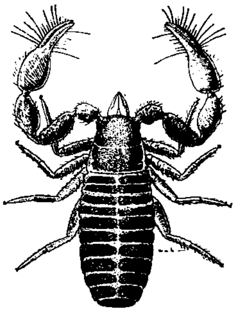
Wilson, E. O. 1971. The Insect Societies. Cambridge, MA: Belknap/Harvard University Press, 548 pp.

Yamamoto, D., J.-M. Jallon, and A. Komatsu. 1997. Genetic dissection of sexual behavior in *Drosophila melanogaster*. Annu. Rev. Entomol. 42: 551–585.

5

Phylum Arthropoda[1]

Arthropods



We are concerned in this book principally with insects, but it is appropriate to point out the place of the insects in the animal kingdom and to include at least a brief account of the animals most closely related to and sometimes confused with the insects.

The insects belong to the phylum Arthropoda, the principal characters of which are as follows:

1. The body segmented, the segments usually grouped in two or three rather distinct regions
2. Paired, segmented appendages (from which the phylum gets its name)
3. Bilateral symmetry
4. A chitinous exoskeleton, which is periodically shed and renewed as the animal grows
5. A tubular alimentary canal, with mouth and anus
6. An open circulatory system, the only blood vessel usually being a tubular structure dorsal to the alimentary canal with lateral openings in the abdominal region
7. The body cavity a blood cavity or hemocoel, the coelom reduced
8. The nervous system consisting of an anterior ganglion or brain located above the alimentary canal, a pair of connectives extending from the brain around the alimentary canal, and paired ganglionated nerve cords located below the alimentary canal
9. Striated skeletal muscles
10. Excretion usually by means of tubes (the Malpighian tubules) that empty into the alimentary canal, the excreted materials passing to the outside by way of the anus
11. Respiration by means of gills, or tracheae and spiracles
12. No cilia or nephridia
13. The sexes nearly always separate

The position of the Arthropoda within the animal kingdom and, indeed, even the reality of the arthropods as a monophyletic group are subjects of active research and controversy. The most serious challenge to the hypothesis of arthropod monophyly began in the 1940s and 1950s (see, for example, Tiegs and Manton 1958) and reached its pinnacle with the publication of *The Arthropoda* by Sidnie Manton in 1977. The essence of this position is that the detailed study of arthropod functional morphology reveals a tremendous amount of diversity, not only in structure, but in the way in which those structures actually work. Manton's own studies dealt largely with mandibular and locomotory mechanisms, and this work was supplemented by other research in embryonic development (Anderson 1973). The structures of modern arthropods are closely integrated and coordinated to form a complex, functional whole, and they were interpreted to be so distinctive between the major groups that no intermediate between them could be conceived that, in turn, could have been functional in the common ancestor. As a result, these features must have evolved independently in the groups that we call *arthropods*. Manton proposed and strongly defended the idea that those groups traditionally placed within Arthropoda had, in fact, independently evolved those characteristics listed at the beginning of this section and, therefore, that the Arthropoda are polyphyletic. This position has been defended recently by Fryer (1997).

The weakness in this argument, of course, is that it addresses the weaknesses in evidence for monophyly

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[1] Arthropoda: *arthro*, joint or segment; *poda*, foot or appendage.

but does not propose a testable alternative hypothesis. To adequately demonstrate that a hypothesis of monophyly is false (that the Arthropoda are not monophyletic), it is necessary to provide evidence showing that one or more "arthropod" taxa are more closely related to a nonarthropod group. No such evidence has been offered. Today, most workers accept that the evidence available is most parsimoniously explained by the hypothesis that the Arthropoda are, indeed, monophyletic.

Traditionally, researchers have held arthropods to be most closely related to the Annelida and the Onychophora. The Annelida, which include the segmented worms (earthworms, marine worms, and leeches) differ from the arthropods in lacking segmented appendages, a chitinous exoskeleton, and a tracheal system. They have a closed circulatory system; the skeletal muscles are not striated; and excretion is by means of ciliated tubes called *nephridia*. Some insect larvae lack appendages and superficially resemble annelids. They can be recognized as insects by their internal organization (different types of circulatory and excretory systems and the presence of tracheae). The Onychophora resemble the arthropods in having (1) segmentation (the body is indistinctly segmented, the segmentation being indicated by the legs, which are unsegmented but bear claws at their apex), (2) a chitinous exoskeleton that is periodically shed and renewed, (3) a tracheal system, and (4) an open circulatory system. They resemble the annelids in having nephridia and unstriated skeletal muscles. The Onychophora are wormlike or sluglike animals, varying in length up to several centimeters. They occur only in the southern hemisphere, where they live in moist situations.

Recent molecular studies, however, have completely changed the perspective on animal relationships (Aguinaldo et al. 1997 and many following works). In the resulting classification, the Arthropoda are grouped together with the Nematoda and a few other small phyla into the Ecdysozoa. This huge group of animals was recognized by similarities in the sequences of ribosomal DNA, but apparently are all characterized by a cuticle that is periodically molted (hence the name: *ecdysis*, escape from; *zoon*, animal). Several subsequent studies, incorporating data from other sources, have confirmed this result. The segmented worms are now placed together in another huge group of protostome animals, the Lophotrochozoa, that includes not only the Annelida, but the Mollusca, Platyhelminthes, and Rotifera. There is, as yet, no consensus on the position of the Onychophora, although most researchers agree they should not be classified within the Arthropoda. This classification is not unequivocally accepted, and the entire subject is a focus of current research.

Classification of the Arthropoda

There are differences of opinion regarding the relationships of the various arthropod groups and the taxonomic level at which they should be recognized. A number of different taxonomic arrangements of these groups have been proposed. We follow here the classification of Barnes (1987) and recognize four major groups within the arthropods as subphyla; this arrangement is as follows (with synonyms in parentheses):

Phylum Arthropoda—arthropods
    Subphylum Trilobita—trilobites (fossils only)
    Subphylum Chelicerata
        Class Merostomata—horseshoe crabs (Xiphosura) and the fossil eurypterids (Eurypterida)
        Class Arachnida—arachnids
        Class Pycnogonida—sea spiders
    Subphylum Crustacea—crustaceans
        Class Cephalocarida
        Class Branchiopoda
        Class Ostracoda
        Class Copepoda
        Class Mystacocarida
        Class Remipedia
        Class Tantulocarida
        Class Branchiura
        Class Cirripedia
        Class Malacostraca
    Subphylum Atelocerata
        Class Diplopoda—millipedes
        Class Chilopoda—centipedes
        Class Pauropoda—pauropods
        Class Symphyla—symphylans
        Class Hexapoda (Insecta)—hexapods

Three phyla sometimes included in the Arthropoda are the Onychophora, Tardigrada, and Pentastomida (= Linguatulida). The Onychophora are somewhat intermediate between the Annelida and the Arthropoda (as noted previously), but the other two groups are somewhat degenerate morphologically (for example, they lack circulatory and excretory organs).

The preceding arrangement of the arthropod groups is based primarily on the character of the appendages (partially the jaws and legs) and the nature of the body regions. The trilobites, crustaceans, and Atelocerata have a pair of antennae (usually two pairs in the crustaceans), whereas the chelicerates lack antennae. The endite lobes at the base of certain appendages (the gnathobase) function as jaws in the trilobites, chelicerates, and crustaceans, whereas (according to Manton 1964, 1977) the Myriapoda and Hexapoda bite

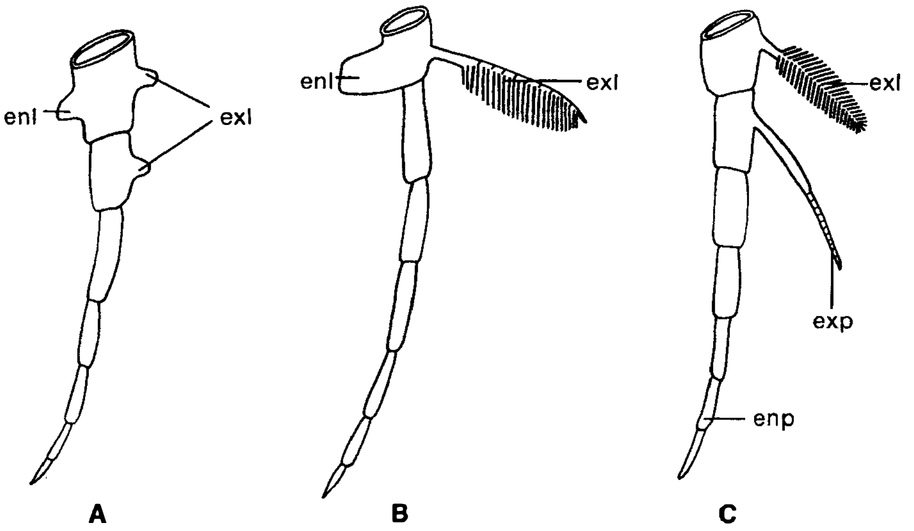

Figure 5–1 Some major variations in arthropod appendages. A, Generalized; B, Trilobite; C, Crustacean. *enl*, endite lobe; *enp*, endopodite; *exl*, exite lobe; *exp*, exopodite.

with the tips of the mandibles. However, recent studies of the expression of the gene *distal-less* in arthropod mouthparts indicate that the mandible of hexapods is also gnathobasic in nature.

Arthropod appendages are subject to a great deal of variation but are basically seven-segmented (Figure 5–1). The basal one or two segments sometimes bear mesal (endite) or lateral (exite) lobes or processes. These lobes or processes frequently have important functions and sometimes have special names. The endite lobes of certain appendages usually have a chewing function in the trilobites, chelicerates, and crustaceans, and an exite lobe of the basal segment often functions as a gill in the trilobites and crustaceans. In the crustaceans, the second segment usually bears a well-developed exite lobe, which is generally segmented and is sometimes as large as or larger than the rest of the appendage, giving the appendage a forked appearance. Such an appendage is spoken of as *biramous*. The exite lobe of the second segment is called the *exopodite*, and the rest of the appendage the *endopodite* (Figure 5–1C).

Subphylum Trilobita[2]

The trilobites lived during the Paleozoic era (see Table 8–2), but were most abundant during the Cambrian and Ordovician periods. These animals were somewhat elongate and flattened, with three rather distinct longitudinal divisions of the body. (The lateral divisions were extensions over the bases of the legs.) Trilobites had a pair of antennae, with the remaining appendages similar and leglike (Figure 5–1B). The anterior part of the body (the preoral region and the first three postoral segments) was covered with a carapace. The legs had an exite lobe or epipodite of the basal segment; this bore a series of lamellae and apparently functioned as a gill (these animals were marine). The endite lobes of the anterior legs apparently functioned as jaws.

Subphylum Chelicerata[3]

Animals belonging to the subphylum Chelicerata lack antennae and typically have six pairs of appendages. The first pair are the chelicerae, and the rest are leglike. Endite lobes of the pedipalps (the second pair of appendages in the arachnids), or the leglike appendages in the horseshoe crabs, function as jaws. The body of a chelicerate usually has two distinct divisions, an anterior region called the *prosoma* (or *cephalothorax*) and a posterior region called the *opisthosoma* (or *abdomen*). The prosoma bears the chelicerae and the leglike appendages. The genital ducts open to the outside near the anterior end of the opisthosoma. Most chelicerates

[2] Trilobita: *tri*, three; *lobita*, lobed (referring to the three longitudinal divisions of the body).

[3] Chelicerata: with chelicerae.

have an extra leg segment, the patella, between the femur and the tibia. The legs are generally uniramous; that is, there is no exite or exopodite.

Class Merostomata[4]

Subclass Eurypterida[5]: The Eurypterida lived during the Paleozoic era, from the Cambrian to the Carboniferous periods. They were aquatic and somewhat similar to the present-day Xiphosura, and some reached a length of more than 2 meters. The prosoma bore a pair of chelicerae, five pairs of leglike appendages, and a pair each of simple and compound eyes; the opisthosoma was 12-segmented, with platelike appendages concealing gills on the first 5 segments, and the telson was either spinelike or lobelike.

Subclass Xiphosura[6]—horseshoe crabs or king crabs: The horseshoe crabs are marine forms and are quite common along the Atlantic Coast from Maine to the Gulf of Mexico. They live in the shallow water and along sandy or muddy shores where they spawn. They feed chiefly on marine worms. Horseshoe crabs are easily recognized by their characteristic oval shell and long, spinelike tail (Figure 5–2).

Class Arachnida—Arachnids[7]

The Arachnida constitute by far the largest and most important class of the Chelicerata (about 65,000 described species, with about 8,000 in North America), and a person studying insects will probably encounter more of them than of any other noninsect group of arthropods. Its members occur almost everywhere, often in considerable numbers.

Most authorities recognize 11 major groups of arachnids (all represented in North America), but not all agree on the names to use for these groups or the taxonomic level they represent. We call these groups *orders* (some would call them *subclasses*) and arrange them as follows (with other names and arrangements in parentheses):

Scorpiones (Scorpionides, Scorpionida)—scorpions
Palpigradi (Palpigrada, Palpigradida, Microthelyphonida)—micro whipscorpions
Uropygi (Thelyphonida, Holopeltidia, Pedipalpida in part)—whipscorpions

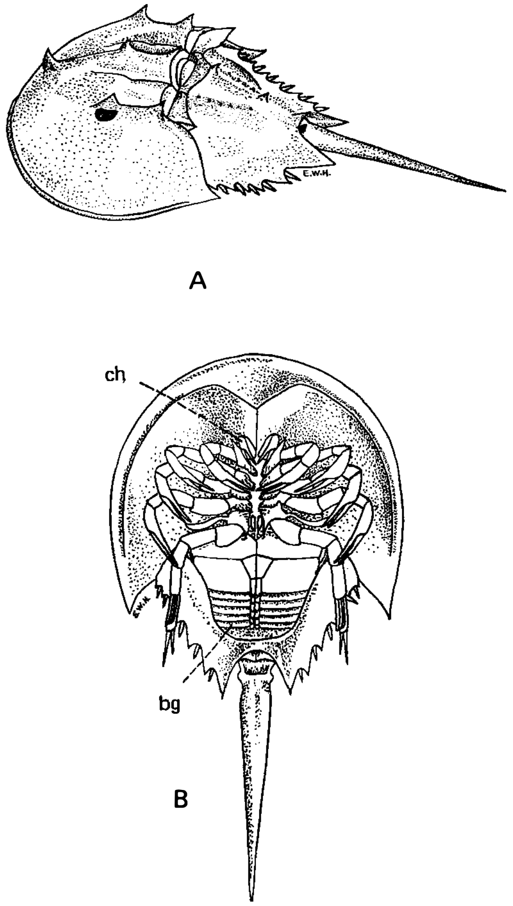

Figure 5–2 A horseshoe crab, *Limulus* sp. (subclass Xiphosura). A, Dorsolateral view; **B**, Ventral view. *bg*, book gills; *ch*, chelicera.

Schizomida (Tartarides, Schizopeltida, Colopyga, Pedipalpida in part)—short-tailed whipscorpions
Amblypygi (Amblypygida, Phrynides, Phryneida, Phrynichida, Pedipalpida in part)—tailless whipscorpions, whipspiders
Araneae (Araneida)—spiders
Ricinulei (Ricinuleida, Meridogastra, Podogonata, Rhinogastra)—ricinuleids
Opiliones (Phalangida, including Cyphophthalmi)—harvestmen
Acari (Acarina, Acarida)—mites and ticks
Pseudoscorpiones (Pseudoscorpionida, Chernetes, Chelonethida)—pseudoscorpions
Solifugae (Solpugida)—windscorpions

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[4] Merostomata: *mero*, part; *stomata*, mouth.

[5] Eurypterida: *eury*, broad; *pterida*, wing or fin.

[6] Xiphosura: *xipho*, sword; *ura*, tail.

[7] Arachnida: from the Greek, meaning a spider.

Key to the Orders of Arachnida

1.	Opisthosoma (abdomen) unsegmented or, if segmented, with spinnerets posteriorly on ventral side (Figures 5–5 and 5–8, ALS,PLS,PMS)	2	
1′.	Opisthosoma distinctly segmented, without spinnerets	3	
2(1).	Opisthosoma petiolate (Figures 5–5 and 5–9 through 5–13)	Araneae	p. 105
2′.	Opisthosoma not petiolate, but broadly joined to prosoma (Figures 5–15 through 5–22)	Acari	p. 129
3(1′).	Opisthosoma with a tail-like prolongation that is either thick and terminating in a sting (Figure 5–3) or slender and more or less whiplike (Figure 5–4A,B); mostly tropical	4	
3′.	Opisthosoma without a tail-like prolongation or with a very short leaflike appendage	7	
4(3).	Opisthosoma ending in a sting (Figure 5–3); first pair of legs not greatly elongated; second ventral segment of opisthosoma with a pair of comblike organs	Scorpiones	p. 104
4′.	Opisthosoma not ending in a sting; first pair of legs longer than other pairs (Figure 5–4A,B); second ventral segment of opisthosoma without comblike organs	5	
5(4′).	Pedipalps slender, similar to legs (Figure 5–4A); minute forms, 5 mm or less in length	Palpigradi	p. 104
5′.	Pedipalps usually much stouter than any of the legs (Figure 5–4B); mostly larger forms	6	
6(5′).	With two median eyes on a tubercle anteriorly and a group of three eyes on each lateral margin; tail long, filiform, and many-segmented; pedipalps nearly straight or curved mesad, extending forward, and moving laterally (Figure 5–4B); body blackish, more than 50 mm in length	Uropygi	p. 104
6′.	Eyes lacking; tail short, one- to four-segmented; pedipalps arching upward, forward, and downward and moving vertically; body yellowish or brownish, less than 8 mm in length	Schizomida	p. 105
7(3′).	Pedipalps chelate (pincerlike) (Figure 5–23); body more or less oval, flattened, usually less than 5 mm in length	Pseudoscorpiones	p. 135
7′.	Pedipalps raptorial or leglike, but not chelate; body not particularly flattened; size variable	8	
8(7′).	Chelicerae very large, usually about as long as prosoma, and extending forward, and body slightly narrowed in middle (Figure 5–4C); color pale yellow to brownish; length 20 to 30 mm; mostly nocturnal desert forms occurring in western United States	Solifugae	p. 135
8′.	Without the preceding combination of characters	9	
9(8′).	First pair of legs very long, with long tarsi; opisthosoma constricted at base; mainly tropical	10	
9′.	First legs similar to the others and (except in the Opiliones) not usually long; opisthosoma not particularly constricted at base	11	
10(9).	Prosoma longer than wide, lateral margins nearly parallel, and with a transverse membranous suture in caudal third; opisthosoma with a very short terminal appendage; length 5–8 mm (see also couplet 6′)	Schizomida	p. 105
10′.	Prosoma wider than long, lateral margins rounded or arched, and without a transverse suture; opisthosoma without a terminal appendage; length variable, up to about 50 mm	Amblypygi	p. 105

11(9′).	Orange-red to brown arachnids, about 3 mm in length, with broad flap at anterior end of prosoma concealing chelicerae; legs not unusually long, animal somewhat mitelike or ticklike in appearance; recorded from Rio Grande Valley of Texas	Ricinulei	p. 128
11′.	Size and color variable, but without broad flap at anterior end of prosoma covering chelicerae; legs variable in length, often very long and slender (Figure 5–14); widely distributed	Opiliones	p. 129

ORDER **Scorpiones**[8]—Scorpions: The scorpions are well-known animals that occur in the southern and western parts of the United States. They are fair-sized arachnids, varying in length up to about 125 mm. The opisthosoma is broadly joined to the prosoma and is differentiated into two portions, a broad seven-segmented mesosoma and a much narrower five-segmented posterior metasoma that terminates in a sting (Figure 5–3). The prosoma bears a pair of eyes near the midline and two to five along the lateral margin on each side. The pedipalps are long and chelate. On the ventral side of the second opisthosomal segment is a pair of comblike structures, the pectines.

Scorpions are largely nocturnal and during the day remain concealed in protected places. When a scorpion runs, the pedipalps are held outstretched and forward, and the posterior end of the opisthosoma is usually curved upward. Scorpions feed on insects and spiders, which they catch with their pedipalps and sometimes sting. The young are born alive and, for a time after birth, ride about on the mother's back. Scorpions grow slowly, and some species require several years to reach maturity. The function of the pectines is not known, but they are believed to be tactile organs.

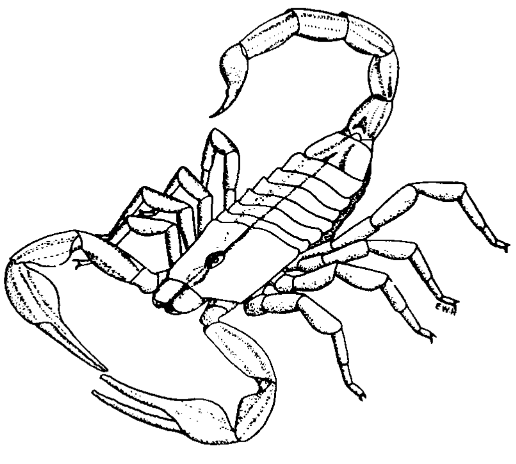

Figure 5–3 A scorpion, 2×.

The effect of a scorpion sting depends primarily on the species of scorpion involved. The sting of most species is painful and usually accompanied by local swelling and discoloration, but it is not dangerous. Of the 40-odd species of scorpions in the United States, only one—*Centruroides sculpturatus* Ewing—is very venomous, and its sting may be fatal. This species is slender and rarely exceeds 65 mm in length. It varies in color from almost entirely yellowish to yellowish-brown with two irregular black stripes down the back. There is a slight dorsal protuberance at the base of the sting. As far as is known, this species occurs only in Arizona.

Scorpions do not ordinarily attack people but will sting quickly if disturbed. In areas where scorpions occur, be careful in picking up boards, stones, and similar objects, and brush off, rather than swat, a scorpion found crawling on your body.

ORDER **Palpigradi**[9]—Micro Whipscorpions: These are tiny arachnids, 5 mm or less in length, somewhat spider-like in appearance but with a long segmented tail (Figure 5–4A). The pedipalps are leglike, and the first pair of legs is the longest. These animals usually live under stones or in the soil. This group is represented in the United States by three species in Texas and California.

ORDER **Uropygi**[10]—Whipscorpions: The whipscorpions are mainly tropical and, in the United States, occur only in the South. They are elongate and slightly flattened, with a slender, segmented tail about as long as the body, and powerful pedipalps (Figure 5–4B); the maximum body length is about 80 mm, and the total length including the tail may be 150 mm or more. They

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[8] Scorpiones: from the Latin, meaning a scorpion.

[9] Palpigradi: *palpi*, palp or feeler; *gradi*, walk (referring to the leglike character of the pedipalps).

[10] Uropygi: *uro*, tail; *pygi*, rump (referring to the whiplike tail).

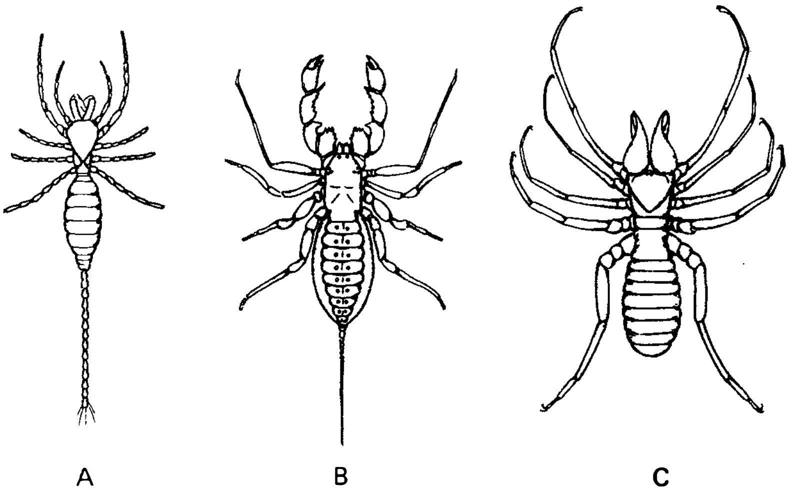

Figure 5–4 Arachnids. A, A micro whipscorpion (Order Palpigradi); **B**, A whipscorpion (Order Uropygi); C, A windscorpion (Order Solifugae). (Courtesy of the Institute of Acarology.)

look somewhat like scorpions but have a very slender "tail" and no sting. The first pair of legs is slender and used as feelers; only the three hind pairs of legs are used in walking. When disturbed, these animals emit (or spray, up to 0.5 meter) a substance with a vinegar-like odor from glands at the base of the tail, and hence they are often called *vinegaroons* (or *vinegarones*). Whipscorpions are nocturnal and predaceous. They are generally found under logs or burrowing in the sand. The eggs are carried in a membranous sac under the opisthosoma, and the young ride around on the back of the female for a time after they hatch. The whipscorpion most likely to be encountered in the southern states is *Mastigoproctus giganteus* (Lucas), which occurs in Florida and the Southwest; it has a body length of 40 to 80 mm and is the largest species in the order.

ORDER **Schizomida[11]—Short-Tailed Whipscorpions:** These animals are somewhat similar to the Uropygi but much smaller and more slender. In addition, the terminal appendage is not long and whiplike; the pedipalps arch upward and forward and move vertically; and there is a transverse suture on the prosoma. The first legs are slender and are not used for walking. The fourth legs are modified for jumping, and in the field these animals superficially resemble small crickets. There are no venom glands or eyes. The eight species of Schizomida in the United States occur in Florida and California. *Trithyreus pentapeltis* (Cook), which occurs in California, is yellowish- to reddish-brown in color and 4.5 to 7.5 mm in length; it lives under rocks and in leaf litter in the desert regions of southern California. A Florida species, *Schizomus floridanus* Muma, is 3.0 to 3.3 mm in length and pale yellowish in color; it lives in crevices in bark and in organic debris, from the Miami area south into the Keys.

ORDER **Amblypygi[12]—Tailless Whipscorpions or Whipspiders:** These arachnids are somewhat spiderlike in appearance, but the opisthosoma is distinctly segmented and, although narrowed at the base, is not petiolate. There are no spinnerets; the pedipalps are large, powerful, and spiny (and are used in capturing prey); and the first legs are very long and whiplike. The prosoma is wider than long and has rounded sides. There are no venom glands. The few North American species vary in length from about 10 to 55 mm and occur chiefly in the southern states. They are found under bark or stones (usually scurrying sideways when disturbed) and sometimes enter houses.

ORDER **Araneae[13]—Spiders:** Spiders are a large, distinct, and widespread group with more than 3,700 described species in North America and more than 38,000 worldwide. The earliest evidence of spiders comes from a 380-million-year-old Devonian fossil (Shear et al. 1989). Spiders occur in many types of habitats and are often very abundant. Typical nondesert

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[11] Schizomida: *schizo*, split (referring to the transverse suture on the prosoma).

[12] Amblypygi: *ambly*, blunt; *pygi*, rump.

[13] Araneae: from the Latin, meaning a spider. This section was written by Jeremy A. Miller and Darrell Ubick.

habitats may support up to 800 spiders per square meter. Point estimates of spider diversity range from 20 species per hectare in the temperate zone to more than 600 species per hectare in tropical forests (Coddington and Colwell 2001).

Unique derived characters that define spiders include cheliceral venom glands (lost in the family Uloboridae), abdominal spinnerets, and the modification of the male pedipalps into sperm transfer organs.

Medically Important Spiders. Although spider bites are widely feared, few species are dangerous to humans. Brown recluse spiders and their relatives (13 North American species including 2 exotics, genus *Loxosceles*, family Sicariidae) and black widow spiders (5 North American species, genus *Latrodectus*, family Theridiidae) are the most medically important spiders in the United States.

Loxosceles (Figures 5–9I, 5–10) lives mostly in the Midwest and Southwest. A species introduced from Europe has been found on the eastern seaboard and elsewhere in the United States, but the venom of this species is relatively mild (Gertsch and Ennick 1983). Brown recluse venom causes a small, dry, irregular necrotic lesion that heals very slowly. Contrary to popular belief, brown recluse bites cannot be conclusively diagnosed from the wound. Serious medical conditions, including Lyme disease, chemical burn, and anthrax infection, have been misdiagnosed as brown recluse bites, delaying proper treatment (Osterhoudt et al. 2002, Sandlin 2002). It is not uncommon for such misdiagnoses to occur outside the range of the brown recluse spider (Vetter and Barger 2002, Vetter and Bush 2002).

Latrodectus (Figure 5–11A) is widespread in the United States. Black widow venom is a neurotoxin. Typical symptoms of envenomation include swelling of the lymphatic nodes, profuse sweating, rigidity of the abdominal muscles, facial contortions, and hypertension. Antivenin is readily available to counteract the effects of *Latrodectus* envenomation. No deaths have been attributed to widow bites in the United States since the 1940s.

Neither *Loxosceles* nor *Latrodectus* species known from North America are aggressive. Unlike groups such as fleas, ticks, biting flies, and bed bugs, spiders do not take blood meals from humans and do not normally bite humans except in self-defense.

Two other spiders have been implicated in causing minor necrotic lesions. Both are introduced from Europe. *Tegenaria agrestis* (Walckenaer) (family Agelenidae) is found in the Pacific Northwest; *Cheiracanthium mildei* Koch (family Miturgidae) is now widespread in human structures in North America. Two other species in North America, *Cheiracanthium inclusum* (Hertz) (family Miturgidae) and *Argiope aurantia* Lucas (family Araneidae) are reported to have a mild neurotoxic venom. Despite their imposing appearance, North American tarantulas (family Theraphosidae) have relatively innocuous venoms. However, they are capable of releasing a cloud of urticating hairs that can cause discomfort in the mucous membranes of mammals.

Silk. The ability to produce silk has evolved independently in several arthropod lineages. However, spiders are the only group to use silk throughout their lives (Coddington and Colwell 2001). In addition to its conspicuous use as a snare to trap prey, silk is used to line burrows, construct retreats and molting chambers, make sperm webs, protect developing eggs, and serve as a dragline. Complex snares, including orb webs, incorporate several distinct types of silk. Some spiders periodically eat their web and are capable of rapidly recycling most of the protein into fresh silk (Peakall 1971). Some spiders, especially small species and immature individuals, use silk for a form of airborne travel called *ballooning*. To balloon, the spider climbs to a high point and releases silk into the air. When the drag on the silk exceeds the spider's mass, the spider releases itself into the air.

Silk is a protein fiber produced in glands that terminate in spigots on the abdominal spinnerets (Figures 5–6, 5–8). In the gland, silk is a water-soluble liquid protein soup. As the silk is spun, it passes through an acid bath (Vollrath and Knight 2001). The acid hardens the silk by causing the molecules to reorient. Complementary regions of the silk molecule align and bond together in multilayered stacks, forming protein crystals. These crystals are interspersed in a matrix of loosely arranged amino acids. The protein crystals give the silk its strength, and the loose matrix provides elasticity (Gosline et al. 1986).

The physical properties of silk are remarkable. Tensile strength is the greatest stress a material will tolerate before failure. Silk is stronger than most natural materials and is about half as strong as steel. However, silk is extremely extensible: It can tolerate substantial distortion (strain) before failure. The product of stress to strain is expressed as toughness and is the total amount of energy a material will absorb before failure. Silk has extremely high toughness; steel tolerates very little distortion in shape, and so is not a very tough material (Figure 5–5).

Anatomy. The body of a spider is divided into two regions, the cephalothorax and the abdomen (Figure 5–6). The abdomen, usually soft and unsclerotized, is attached to the cephalothorax by a narrow pedicel. The

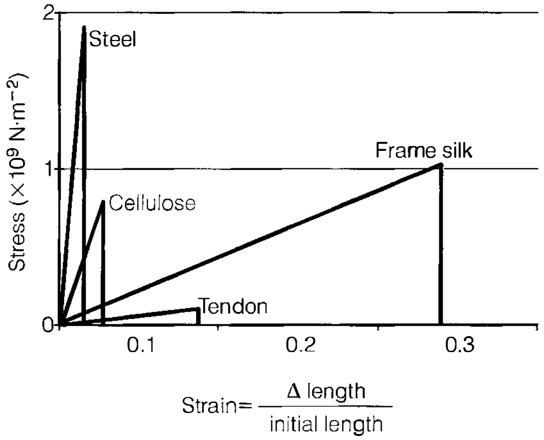


Figure 5–5 Structural properties of silk compared to other materials (From Gosline *et al.* 1986).

cephalothorax bears the eyes, mouthparts, legs, pedipalps, and stomach. The abdomen contains the primary reproductive structures, respiratory system, intestine, anus, silk glands, and spinnerets.

The cephalothorax is covered dorsally by the **carapace** and ventrally by the **sternum**. Anterior to the sternum is a small sclerite called the **labium**, which may be fused to the sternum. Spiders primitively have eight simple eyes, but some taxa have fewer eyes. Eye number and arrangement is important in identifying spiders. The area between the anterior eye and the edge of the carapace is the **clypeus**.

The first pair of appendages is called the **chelicerae**. Chelicerae have two segments, a base and a fang. The opening for the poison gland is located near the tip of the fang. The base may be quite robust. The base may receive the fang in a furrow, which is usually lined with rows of teeth. In some families, the cheliceral bases may be fused by a membranous lamella

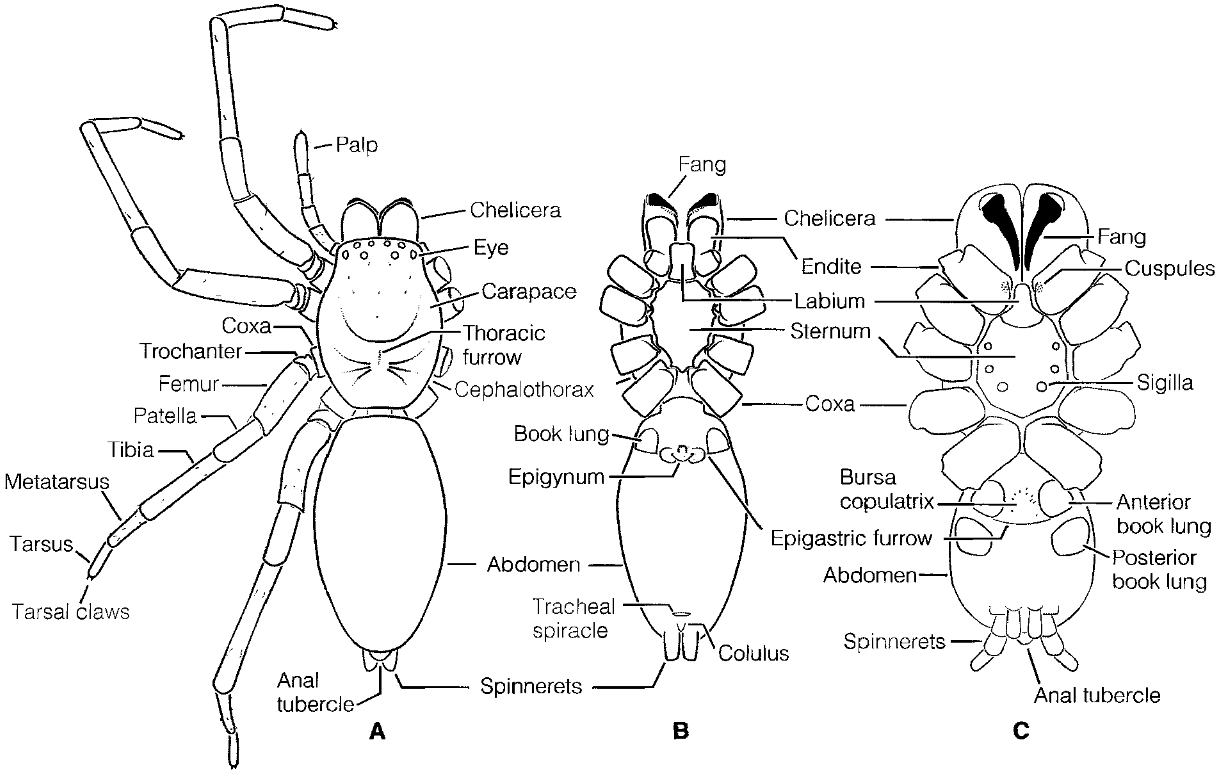


Figure 5–6 Structural characteristics of spiders. A, Dorsal view (generalized); B, Ventral view, araneomorph; C, Ventral view, mygalomorph.

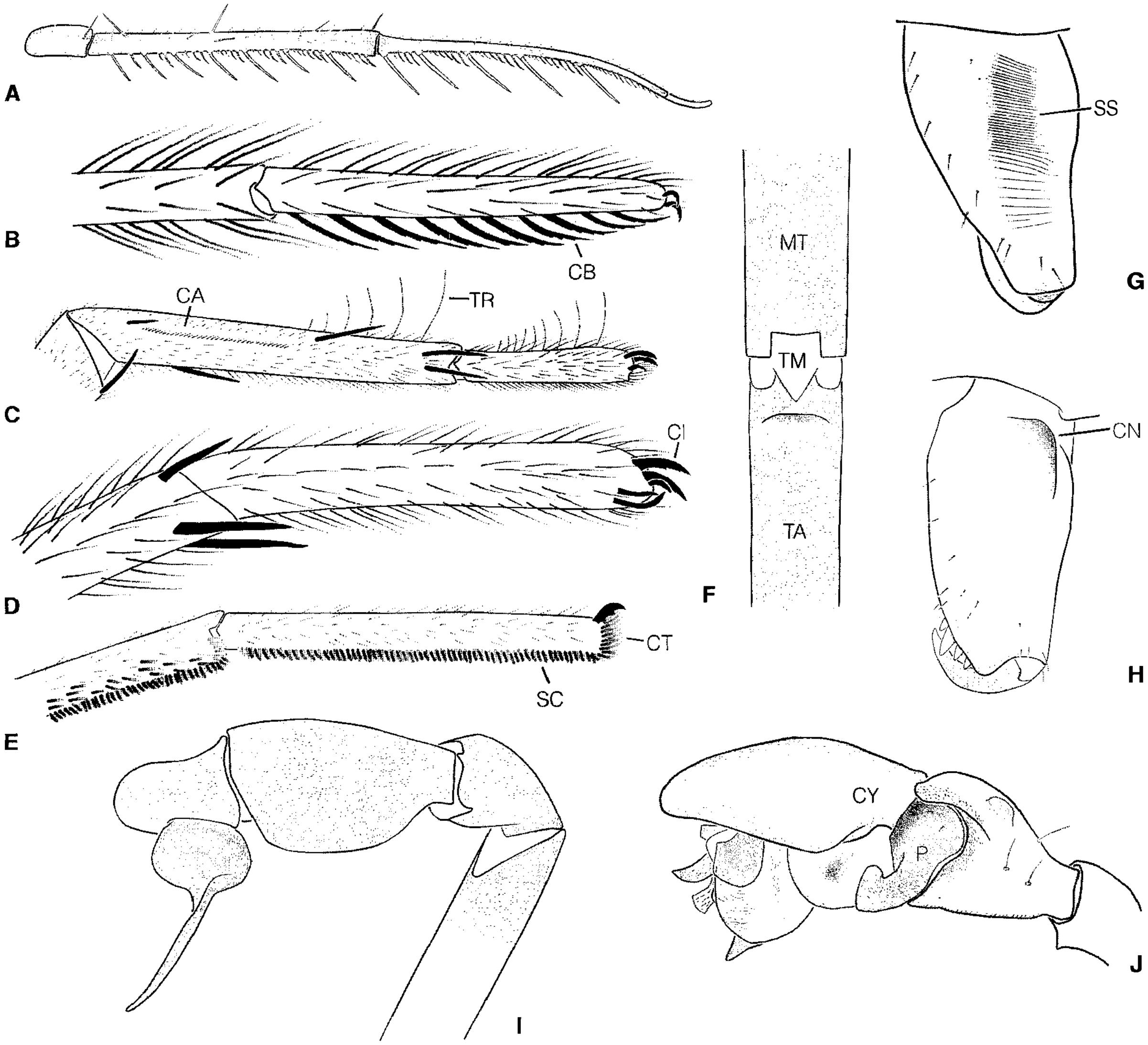


Figure 5–7 Legs, chelicerae, and male palp characters of spiders. A, First leg of *Mimetus puritanus* Chamberlin (Mimetidae); B, Fourth metatarsus of *Achaearanea tepidariorum* (C. L. Koch) (Theridiidae); C, Fourth tarsus and metatarsus of *Callobius deces* (Chamberline and Ivie) (Amaurobiidae); D, Tarsus of *Araneus diadematus* Clerck (Araneidae); E, Tarsus of *Tibellus oblongus* (Keyserling) (Philodromidae); F, Trilobe membrane between metatarsus and tarsus of *Heteropoda venatoria* (L.) (Sparassidae); G, Stridulatory striae on lateral face of chelicera, *Mermessus dentiger*; H, Chelicera of *Araneus diadematus* showing condyle on proximolateral part. I, Male palp of a haplogyne spider, *Latrodectus reclusa* Gertsch and Mulaik (Sicariidae); J, Palp of an entelegyne male, *Mermessus dentiger* O. Pickard-Cambridge (Linyphiidae). *CA*, calamistrum; *CB*, ventral comb of setae; *Cl*, claws; *CN*, condyle; *CT*, claw tufts; *CY*, cymbium; *MT*, metatarsus; *P*, paracymbium, *SC*, scopula; *SS*, stridulatory striae; *TA*, tarsus; *TM*, trilobe membrane, *TR*, trichobothrium.

(Figure 5–9F,I). The basal segment of the chelicera sometimes bears a small rounded lateral prominence (the condyle) at its base (Figure 5–7H, CN). Some spiders have a series of filelike ridges on the lateral surface of the chelicerae (Figure 5–7G, SS). Spiders may use a plectrum on the pedipalp to stridulate against these ridges.

The second pair of appendages is the **pedipalps**. The pedipalps are somewhat leglike, except that they lack a metatarsus and have only one terminal claw (lost in some spiders). The basal segment, the endite, is enlarged and forms part of the oral cavity. The anterior margin of the endite usually has a **serrula** for cutting into prey. The labium lies between the two endites.

Adult male spiders have their pedipalps (or simply palpus) modified into sperm transfer organs. The form of the male palpal organ is extremely variable and is critical in spider taxonomy (Figures 5–7I,J). Minimally, the palpal organ consists of a bulb containing a sperm duct and a terminal embolus. The bulb is attached to the palpal tarsus, which is called the **cymbium** (Figure 5–7J, CY). The cymbium may be ventrally excavated, partially enclosing the palpal bulb. A paracymbium is an appendage arising from the cymbium (Figure 5–7J, P). The testes are located in the abdomen. There is no connection between the testes and the pedipalps. Instead, sperm is extruded from the epigastric furrow. A sperm web is typically spun to receive the sperm. To transfer the sperm, the spider inserts his embolus into the sperm droplet and draws the fluid into the palpal organ, probably by capillary action. During copulation, the male transfers his sperm to the female by inserting the embolus into the female genitalia.

The four pairs of ambulatory legs, numbered I–IV from front to back, have seven segments (coxa, trochanter, femur, patella, tibia, metatarsus, and tarsus), and each leg bears two or three terminal claws. Two claws are paired; the third, if present, is smaller and set between them. The tip of the tarsus may have numerous setae, the claw tuft, which may obscure the claws (Figure 5–7E, CT). Usually claw tufts are present only in two-clawed spiders, but there are exceptions (noted later). In some spiders, the ventral part of the tarsus (and sometimes the metatarsus) is covered with a very dense field of modified hairs, the scopula (Figure 5–7E, SC). This structure may allow spiders to walk on smooth vertical surfaces. Various leg segments may have trichobothria (Figure 5–7C, TR). These long, straight hairs are sensitive to air currents. The position and number of trichobothria can be a useful taxonomic character.

Near the anterior end of the abdomen on the ventral side is a transverse groove called the **epigastric furrow**, which at its midpoint bears the gonopore. The female stores sperm received from males in spermathecae just anterior to this furrow. She fertilizes her eggs just before exuding them through the epigastric furrow.

On the anterolateral portion of the epigastric furrow are the anterior respiratory organs, the book lungs (rarely lost or modified in some families). The book lungs consist of alternating layers of sheetlike air pockets and hemolymph-filled (blood-filled) lamellae. The air- and hemolymph-filled regions are incredibly thin, which facilitates gas exchange. Primitively, spiders had a second pair of book lungs immediately posterior to the anterior pair. In most spiders, the posterior respiratory organs are modified into a tracheal system. The tracheal system opens to the environment via the tracheal spiracle, which may be a pair of ventrolateral slits or a single ventral slit. The single tracheal spiracle usually lies just anterior to the spinnerets, but in some spider taxa is closer to the epigastric furrow.

The spinnerets are usually on the posterior part of the abdomen (Figure 5–8). Extant spiders have no more than six functional spinnerets: the anterior lateral, posterior median, and posterior lateral pairs. The anterior median spinnerets are not functional in any living spider. However, a platelike spinning organ called the cribellum (Figure 5–8A, CR) is believed to be derived from the anterior median spinnerets. The cribellum is lost in many araneomorph spiders, but a vestige called the colulus may remain (Figure 5–8B-E). Posterior to the spinnerets is the anal tubercle (Figure 5–6A,C). This structure is usually quite small but is enlarged and modified in oecobiids.

Reproduction and Development. The two sexes of spiders often differ considerably in size, the female being larger and heavier, and the male being smaller but with relatively long legs. Mating is often preceded by elaborate courtship, which may involve a variety of body or pedipalp movements or stridulation. In some cases, the male may present the female with a dead insect or other nuptial gift before mating. Males usually do not live long after mating.

Fertilized eggs are deposited in a silk sac. These sacs vary in their construction. They may be suspended in a web, deposited in some sheltered location, or carried about by the female. The number of eggs in a sac varies between 1 and over 2,000. The eggs usually hatch soon after they are laid, but if the eggs are laid in the autumn the young spiders may remain in the sac until the following spring.

Spiders undergo very little metamorphosis during their development. When hatched, they usually look like miniature adults but without developed genitalia. If legs are lost during development, they can usually be regenerated (Vollrath 1991). The point at which legs usually break off can be a useful taxonomic character. Spiders generally molt from 3 to 15 times during their

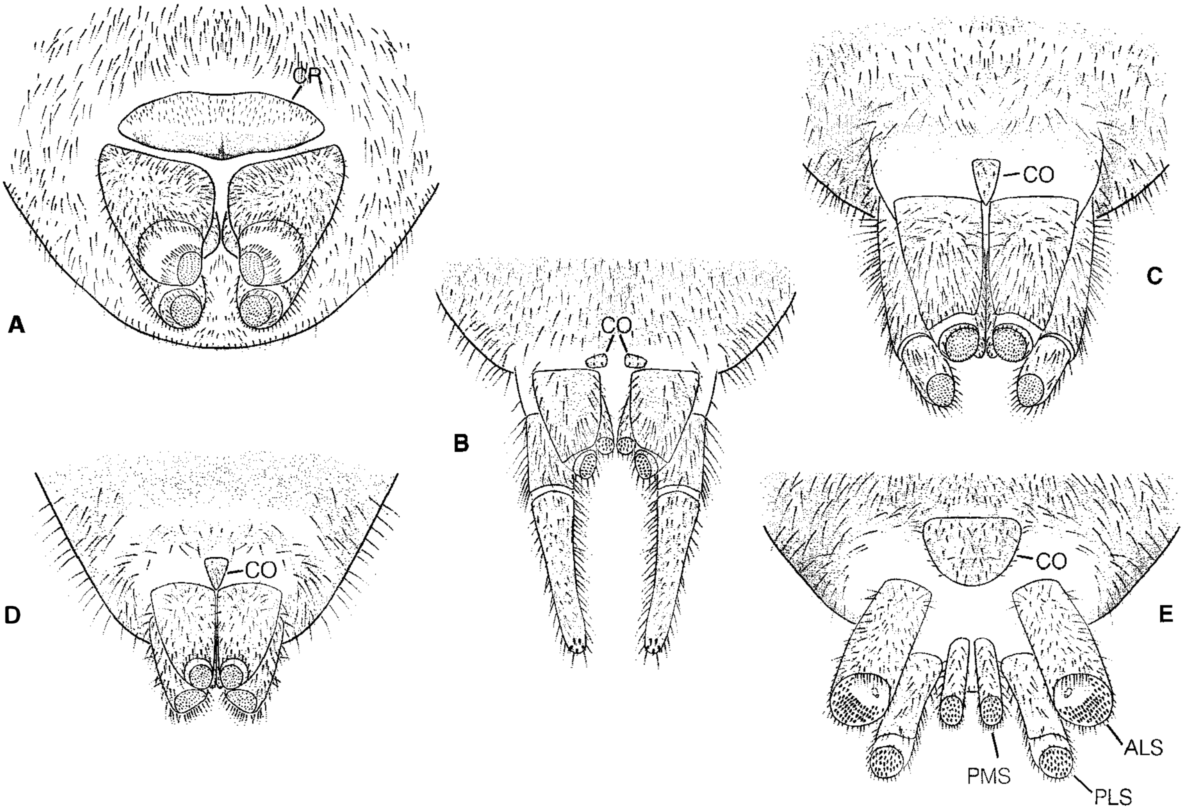


Figure 5–8 Abdominal characters of spiders. A, Spinnerets of *Callobius deces* (Chamberlin and Ivie) (Amaurobiidae); B, Spinnerets of *Agelenopsis oregonensis* Chamberline and Ivie (Agelenidae); C, Spinnerets of *Cheiracanthium meldei* L. Koch (Miturgidae); D, Spinnerets of *Clubiona obesa* Hentz (Clubionidae); E, Spinnerets of *Scotophaeus blackwalli* (Thorell) (Gnaphosidae). *ALS*, anterior lateral spinnerets; *CO*, colulus; *CR*, cribellum; *PLS*, posterior lateral spinneret; *PMS*, posterior median spinneret.

growth to maturity; males typically undergo fewer molts than females. Female mygalomorphs and filistatids continue to molt once or twice a year as long as they live. Most spiders live 1 or 2 years, but mygalomorphs often take several years to mature, and some females may live as long as 20 years.

Ecology. All spiders are predaceous and feed mainly on insects. Some spiders may occasionally feed on small vertebrates. The prey is usually killed or disabled by the poison injected into it by the spider bite. Different spiders capture their prey in different ways. The wolf spiders and jumping spiders actively forage and pounce on their prey. Many crab spiders are sit-and-wait predators, waiting for their prey on flowers and feeding on visiting pollinators. Many spiders capture their prey in webs. A few spiders are kleptoparasites, living in the webs of other spiders and stealing prey from the host's web. A small number of spider species have some degree of social organization. Social spiders may cooperate to build webs of several cubic meters and feed communally on the large prey items they subdue.

Spiders play an important role in nearly all terrestrial ecosystems. They are generally quite numerous, and their predation impact keeps in check the numbers of many other animals, particularly insects. They are, in turn, preyed on by various other animals, particularly wasps. There is growing evidence that spiders can keep populations of pest insects in check in agroecosystems (Wise 1993, Riechert 1999). Conventional integrated pest management programs tend to rely on predators and parasitoids that attack specific pest species, but dense populations of generalist predators, including spiders, can effectively limit some pest populations. However, broad-spectrum insecticides can be more effective in killing spiders than they are in killing the pests being targeted. Agricultural practices that encourage increases in spider density can greatly decrease the need for chemical insecticides without loss in crop yield (Riechert 1999). Fear of spiders (arachnophobia) is one of the most common phobias is Western culture. However, spiders perform a service by destroying noxious insects and do not damage household items. As pointed out earlier, the venomous nature of spiders is generally greatly exaggerated. Most spiders do not bite if handled carefully.

Classification of Spiders

Spiders are divided into two suborders: Mesothelae and Opisthothelae. The Mesothelae are currently restricted to southeastern Asia and Japan. These relict taxa retain many features of primitive spiders, such as abdominal segmentation and ventral spinnerets. The vast majority of spiders belongs to the suborder Opisthothelae, which itself is divided into two infraorders, Mygalomorphae and Araneomorphae. Both occur in North America. A few basal mygalomorphs have vestiges of abdominal segmentation in the form of abbreviated tergites. A sclerotized scutum covering part of the abdomen is found sporadically among araneomorph spider taxa and is not derived from primitive abdominal segmentation. Mesothele and mygalomorph spiders have chelicerae oriented so that the fangs are more or less parallel (Figure 5–6C); araneomorph spiders usually have opposing fangs (Figure 5–6B), although some taxa have secondarily modified chelicerae. Mesotheles, mygalomorphs, and the most basal groups of araneomorph spiders have two pairs of book lungs. In North America, only hypochilids among the araneomorphs retain the posterior pair of book lungs. In most araneomorph spiders, the posterior pair of book lungs is modified into a tracheal system (Figure 5–6B). Secondary modifications of the respiratory system occur in some derived groups of araneomorph spiders.

Individual species can produce up to seven distinct types of silk, each with a specialized function, such as dragline production, egg sac construction, and both the adhesive and nonadhesive parts of a web. Basal araneomorph spiders produce adhesive silk from a platelike cribellum just anterior to the spinnerets (Figure 5–8A, CR). The cribellum is covered in tiny spigots. Cribellate silk consists of hundreds of very fine, dry silk fibers around a few thicker core fibers. The physical basis of stickiness in cribellate silk is not well understood, but the adhesive force is proportional to the surface area contact between the silk and the object being held (Opell 1994). Cribellate silk is combed out from the cribellum using the **calamistrum**, a group of specialized, curved setae on the metatarsus of the fourth leg (Figure 5–7C, CA), which may be a single row of setae, two rows, or an oblong field. Mature male cribellate spiders lose the ability to make cribellate silk and typically retain only a vestige of the cribellum and calamistrum. The cribellum and calamistrum have been lost numerous times in spider evolution. A well-known example of ecribellate sticky silk comes from araneoid spiders, the ecribellate orb-weavers and their descendents. Araneoid sticky silk consists of a pair of core lines dotted with sticky droplets. Adult male spiders rarely spin prey-capture webs and sometimes lose the ability to produce sticky silk.

Spider taxonomy is based heavily on characters of the genitalia. For this reason, juvenile spiders are usually impossible to identify to species unless they are found associated with adults or unless the local fauna is very well known. Determining whether a spider is an adult can be difficult for the beginner. Adult female spiders usually have a sclerotized plate called an epigynum (Figure 5–6B) located near the epigastric furrow between the anterior respiratory organs (the genital region). In some spiders (for example, lycosids), a rudimentary, nonfunctional plate may be visible during late-stage juvenile development. Female spiders sometimes lack an external sclerotized plate and can be easily confused with juveniles. In such spiders, adult females differ by the presence of dense hairs in the genital region; hairs in the genital region are undifferentiated in juveniles. All adult female spiders have a set of spermathacae, which can be examined by carefully dissecting the integument anterior to the epigastric furrow. Few student collections will contain many species where the female lacks and epigynum. Adult male spiders always have the distal segments of the pedipalp modified. Late-stage juvenile males may have a swollen palpal tarsus, indicating that the palpal organ is developing inside.

Infraorder Mygalomorphae
  Antrodiaetidae—folding-door spiders
  Atypidae—purse-web spiders
  Mecicobothriidae
  Dipluridae
  Ctenizidae
  Cyrtaucheniidae
  Nemesiidae
  Theraphosidae—tarantulas

Infraorder Araneomorphae
  Hypochilidae—lampshade spiders
  Haplogynae
    Filistatidae
    Caponiidae
    Dysderidae
    Segestriidae

  - Oonopidae
  - Pholcidae—cellar spiders
  - Diguetidae
  - Plectreuridae
  - Ochyroceratidae
  - Leptonetidae
  - Telemidae
  - Sicariidae
  - Scytodidae—spitting spiders
- Entelegynae
  - Eresoidea
    - Oecobiidae
    - Hersiliidae
- Orbiculariae
    - Uloboridae—hackled-band orb-weavers
    - Deinopidae—ogre-faced spiders
    - Araneidae
    - Tetragnathidae
    - Theridiosomatidae
    - Symphytognathidae
    - Anapidae
    - Mysmenidae
    - Mimetidae—pirate spiders
    - Theridiidae—cobweb spiders
    - Nesticidae
    - Linyphiidae
    - Pimoidae
  - Titanoecidae
  - RTA Clade
    - Dictynidae
    - Zodariidae
    - Hahniidae
    - Agelenidae
    - Cybaeidae
    - Desidae
    - Amphinectidae
    - Amaurobiidae
    - Tengellidae
    - Zorocratidae
    - Superfamily Lycosoidea
      - Ctenidae—wandering spiders
      - Zoropsidae
      - Miturgidae
      - Oxyopidae—lynx spiders
      - Pisauridae—nursery-web and fishing spiders
      - Trechaleidae
      - Lycosidae—wolf spiders
    - Clade Dionycha
      - Clubionidae
      - Anyphaenidae
      - Corinnidae
      - Liocranidae
      - Zoridae
      - Gnaphosidae
      - Prodidomidae
      - Homalonychidae
      - Selenopidae
      - Sparassidae—giant crab spiders
      - Philodromidae
      - Thomisidae
      - Salticidae—jumping spiders

Key to Spider Families of North America

This key is adapted from D. Ubick, in preparation, Key to Nearctic Spider Families. In D. Ubick, P. Paquin, P. E. Cushing, and V. Roth (Eds.), Spiders of North America: A Guide to Genera (available in January 2005 from the American Arachnological Society). The following abbreviations are used in the key. *Eyes:* AER = anterior eye row; PER = posterior eye row; AME = anterior median eyes; ALE = anterior lateral eyes; PME = posterior median eyes; PLE = posterior lateral eyes; LE = lateral eyes. *Spinnerets:* AMS = anterior median spinnerets; ALS = anterior lateral spinnerets; PMS = posterior median spinnerets; PLS = posterior lateral spinnerets. *Measurements:* L = length; W = width; PT/C is the ratio of the patella+tibia length divided by carapace length. The term **procurved** refers to a line in which the ends are anterior to the center of the line; a **recurved** line has the ends posterior to the middle.

1. Chelicerae paraxial, fangs parallel (Figure 5–6C); with 2 pairs of book lungs (Figure 5–6C); never with cribellum or colulus; with 8 eyes; legs stout (PT/C < 2) (Mygalomorphae) 2

1′. Chelicerae diaxial, fangs opposing each other or oblique (Figure 5–6B); usually with at most 1 pair of book lungs (Figure 5–6B), if with 2 pairs of book lungs then with cribellum (Figure 5–8A) and slender legs (PT/C = 3 to 5); cribellum or colulus may be present; with 8 or fewer eyes; leg thickness variable (Araneomorphae) 11

2(1). Abdomen with 1–3 tergites; anal tubercle separated from spinnerets 3

2′.	Abdomen without tergites; anal tubercle adjacent to spinnerets	5	
3(2).	Endites long, ¾ width of sternum; labium and sternum fused; thoracic furrow (Figure 5–6A) quadrangular or suboval; eastern United States	Atypidae	p. 120
3′.	Endites short, at most ½ width of sternum; labium and sternum separated by a suture, groove, or at least a depression; thoracic furrow longitudinal or rounded and pitlike; widespread	4	
4(3′).	Distal segment of PLS slender, at least 5× as long as basal width, tapering to a point, flexible, pseudosegmented; Washington to California, Arizona	Mecicobothriidae	p. 120
4′.	Distal segment of PLS stouter, about 3× as long as wide, neither flexible nor pseudosegmented; widespread in distribution	Antrodiaetidae	p. 120
5(2′).	Tarsi with 2 claws and claw tufts (Figure 5–7E). Florida to southwestern United States	Theraphosidae	p. 122
5′.	Tarsi with 3 claws, lacking claw tufts (Figure 5–7D). widespread in distribution	6	
6(5′).	PLS long, at least ½ carapace length, and slender, length of distal segment > 2× width	7	
6′.	PLS short, at most ½ carapace length, and stout, length of distal segment < 2× width	8	
7(6).	Endites with cuspules (Figure 5–6C); cheliceral inner surface with row of 4–7 short, black, rodlike setae; thoracic furrow transverse; PLS ½ to ⅔× carapace length; size 16–23 mm; living in open burrows; California	Nemesiidae (*Calisoga*)	p. 122
7′.	Endites lacking cuspules; cheliceral inner surface without row of black, rodlike setae; thoracic furrow pitlike or longitudinal; PLS at least ¾× carapace length; size 2.5–17 mm; living in silken tubes or on sheet webs; British Columbia to Oregon, Arizona to Texas, North Carolina, Tennessee	Dipluridae	p. 120
8(6′).	Abdomen posteriorly truncated, sclerotized, with longitudinal grooves; southeastern United States	Ctenizidae (*Cyclocosmia*)	p. 120
8′.	Abdomen unmodified, posteriorly rounded, not sclerotized, and without grooves	9	
9(8′).	Females with a dense scopula on tarsus I (Figure 5–7E); cheliceral promargin toothed, retromargin of chelicera with row of short, stout, rounded tubercles; Texas	Cyrtaucheniidae (*Eucteniza*)	p. 122
9′.	Males or females with tarsus I lacking scopula, but with lateral spines; if tarsus I with a weak scopula and lacking spines, then retromargin of chelicera without teeth (but may have a few denticles); widespread in distribution	10	
10(9′).	Both promargin and retromargin of chelicera toothed; thoracic furrow strongly procurved; anterior tarsi and metatarsi of female with lateral rows of short, thornlike spines	Ctenizidae (in part)	p. 120
10′.	Only promargin of chelicera toothed; thoracic furrow varying from strongly procurved to straight; anterior tarsi and metatarsi of female with few spines, these usually long and slender	Cyrtaucheniidae (in part)	p. 122
11(1′).	Cribellum (Figure 5–8B-E) and calamistrum absent	12	
11′.	Cribellum (Figure 5–8A) and calamistrum (Figure 5–7C) present	14	
12(11).	With 8 eyes	13	
12′.	With fewer than 8 eyes	27	

13(12).	Tarsi 3-clawed, scopulae and claw tufts absent (Figure 5–7D); mostly web builders; if legs are slender and relatively delicate, assume tarsi are 3-clawed	51	
13′.	Tarsi 2-clawed, usually with scopulae and claw tufts (Figure 5–7E); if claw tufts are present, assume tarsi are 2-clawed	81	
14(11′).	With 2 pairs of book lungs (Figure 5–6C)	Hypochilidae (*Hypochilus*)	p. 122
14′.	With 1 pair of book lungs (Figure 5–6B)	15	
15(14′).	With fewer than 8 eyes; cribellum entire	16	
15′.	With 8 eyes; cribellum entire or divided	17	
16(15).	With 4 eyes; leg I greatly enlarged; south Texas	Uloboridae (*Miagrammopes*)	p. 124
16′.	With 6 eyes; leg I not enlarged; widespread in distribution	Dictynidae (*Lathys*)	p. 126
17(15′).	PME huge, several times the diameter of remaining eyes (Figure 5–9G)	Deinopidae (*Deinopis*)	p. 124
17′.	PME not so enlarged	18	
18(17′).	Eyes clustered on central mound, occupying $< \frac{1}{2}$ width of cephalon	19	
18′.	Eyes spread across carapace, occupying $> \frac{1}{2}$ width of cephalon	20	
19(18).	Anal tubercle enlarged and fringed with long setae; chelicerae free; entelegyne (epigynum present)	Oecobiidae (*Oecobius*)	p. 124
19′.	Anal tubercle not so modified; chelicerae fused; haplogyne (epigynum absent)	Filistatidae	p. 122
20(18′).	Anterior tibia with at least 4 pairs of ventral spines	21	
20′.	Anterior tibia with fewer ventral spines	22	
21(20).	Anterior tibia with 4–5 pairs of ventral spines; PER straight to weakly procurved; tarsi II–IV with 2 claws; body unicolorous; Arizona to Texas	Zorocratidae (*Zorocrates*)	p. 127
21′.	Anterior tibia with 6–7 pairs of ventral spines; PER recurved; all tarsi with 2 claws; body patterned; California (introduced)	Zoropsidae (*Zoropsis*)	p. 127
22(20′).	Calamistrum extends over more than half the length of metatarsus IV	23	
22′.	Calamistrum extends over no more than half the length of metatarsus IV	25	
23(22).	Femora II–IV with rows of long trichobothria; metatarsus IV dorsally concave and with ventral row of short spines extending to tip of tarsus; cribellum entire	Uloboridae (in part)	p. 124
23′.	Femora II–IV without rows of long trichobothria; metatarsus IV not so modified and without ventral row of short spines; cribellum divided or entire	24	
24(23′).	Endites converging apically; cribellum usually entire; legs usually without spines	Dictynidae (in part)	p. 126
24′.	Endites parallel; cribellum divided; legs with spines	Titanoecidae (*Titanoeca*)	p. 126
25(22′).	Cheliceral margins with 5 to 7 stout teeth; male palpus with embolus threadlike, enclosed in membranous conductor; California, Texas to Florida	Amphinectidae (*Metaltella*)	p. 126
25′.	Cheliceral margins usually with no more than 4 teeth, if more, then teeth small and slender; male palpus with embolus variable; widespread in distribution	26	
26(25′).	AME 1.4× larger than ALE; male palpus with embolus long and sigmoid, enclosed in membranous conductor	Desidae (*Badumna*)	p. 126

26′.	AME at most 1.2× larger than ALE; male palpus with embolus usually short and stout, if long, then arcuate, never enclosed in conductor	Amaurobiidae (in part)	p. 126
27(12′).	Eyes completely lacking (but may have small eye spots)	28	
27’.	At least 2 eyes present	34	
28(27).	Anterior tibia with 2–3 pairs of ventral spines	29	
28′.	Anterior tibia with few scattered ventral spines or none	30	
29(28).	ALS contiguous, longer than PLS	Cybaeidae (in part)	p. 126
29′.	ALS slightly separated, shorter than PLS	Dictynidae (in part)	p. 126
30(28’).	Male palp with exposed bulb (Figure 5–7I), female lacking epigynum (haplogynes)	31	
30′.	Male palp with bulb enclosed by cymbium (Figure 5–7J), female with epigynum (entelegynes)	32	
31(30).	Abdomen with anterodorsal sclerotized ridge; with a pair of tracheal spiracles between epigastric furrow and spinnerets; colulus pentagonal, wider than ALS; California	Telemidae (*Usofila*)	p. 123
31′.	Abdomen without anterodorsal sclerotized ridge; with one tracheal spiracle near spinnerets; colulus not so modified; Texas, Georgia	Leptonetidae (in part)	p. 123
32(30′).	Tarsus IV lacking ventral comb; retromargin of chelicera toothed; chelicera usually with stridulatory file on outer face (Figure 5–7G); leg break at patella–tibia joint	Linyphiidae (in part)	p. 126
32′.	Tarsus IV with ventral comb of serrated setae (Figure 5–7B); retromargin of chelicera edentate or with small denticles; chelicera without stridulatory file; leg break at coxa–femur joint	33	
33(32′).	Retromargin of chelicera edentate, lacking both teeth and denticles; male palp with inconscpicuous paracymbium; southern Arizona	Theridiidae (*Thymoites*)	p. 125
33′.	Retromargin of chelicera with small denticles; male palp with large retrolateral paracymbium; California, Texas, Appalachian Mountains	Nesticidae (in part)	p. 126
34(27′).	Two eyes present	Caponiidae (in part)	p. 122
34′.	More than 2 eyes present	35	
35(34′).	Four eyes present	36	
35′.	Six eyes present	37	
36(35).	Two eyes pigmented; size 0.6 mm; litter spiders; Florida	Symphytognathidae (*Anapistula*)	p. 125
36′.	All eyes unpigmented; size 3.6 mm; cave spiders; Tennessee	Nesticidae (*Nesticus*)	p. 126
37(35′).	Male palp with exposed bulb, not enclosed by cymbium (Figure 5–7I); female lacking epigynum, but may have some sclerotization at epigastric area (haplogynes)	38	
37′.	Male palp with bulb partially enclosed by cymbium (Figure 5–7J), female with epigynum (entelegynes)	48	
38(37).	Chelicerae fused at base (Figure 5–9F)	39	
38′.	Chelicerae not fused at base, can be moved apart (Figure 5–9E)	42	
39(38).	Eyes in 2 triads	Pholcidae (in part)	p. 123
39′.	Eyes in 3 dyads (Figure 5–9G)	40	
40(39’).	Carapace strongly convex	Scytodidae (*Scytodes*)	p. 123
40′.	Carapace flat	41	
41(40′).	PER strongly recurved; carapace pear-shaped (Figure 5–9I)	Sicariidae (*Loxosceles*)	p. 123
41′.	PER slightly recurved; carapace oval	Diguetidae (*Diguetia*)	p. 123

42(38').	Size >5 mm; tracheal spiracles paired, conspicuous, located near book lung openings (Figure 5–9H)	43	
42'.	Size < 5 mm; tracheal spiracles inconspicuous, if paired, then not near book lungs	44	
43(42).	Tarsi with 2 claws; leg III not anteriorly directed	Dysderidae (*Dysdera*)	p. 122
43'.	Tarsi with 3 claws; leg III anteriorly directed	Segestriidae	p. 123
44(42').	Abdomen with sclerotized ridge on anterior dorsal surface	Telemidae (*Usofila*)	p. 123
44'.	Abdomen without sclerotized ridge	45	
45(44').	Abdomen with 1 or 2 scuta	Oonopidae (in part)	p. 123
45'.	Abdomen without scuta	46	
46(45').	Legs relatively long ($PT/C > 1.5$); PME usually posteriorly displaced from LE, if eyes contiguous then occupying less than $\frac{1}{2}$ cephalon width	Leptonetidae (in part)	p. 123
46'.	Legs shorter ($PT/C \approx 1$); eyes in transverse arrangement, if contiguous then occupying more than $\frac{1}{2}$ cephalon width	47	
47(46').	Eyes in compact group; if in transverse row, then femur IV enlarged; colulus absent; widespread in distribution	Oonopidae (in part)	p. 123
47'.	Eyes in transverse row; femur IV not enlarged; colulus large, broad; southern Florida	Ochyroceratidae (*Theotima*)	p. 123
48(37').	Tibia I with 2 to 3 pairs of ventral spines	49	
48'.	Tibia I with fewer ventral spines	50	
49(48).	ALS contiguous, longer than PLS; eyes small, widely separated	Cybaeidae (*Cybaeozyga*)	p. 126
49'.	ALS slightly separated, shorter than PLS; eyes larger, in two triads of contiguous eyes	Dictynidae (in part)	p. 126
50(48').	Tarsus IV with ventral comb of serrated bristles (Figure 5–7B); male palpus with large, rigid basal paracymbium	Nesticidae (in part)	p. 126
50'.	Tarsus IV without ventral comb; male palpus with smaller basal paracymbium flexibly attached by membrane (Figure 5–7J)	Linyphiidae (in part)	p. 126
51(13).	Male palpus with bulb exposed, not enveloped by cymbium (Figure 5–7I); female without epigynum (haplogynes)	52	
51'.	Male palpus with bulb partially enveloped by cymbium (Figure 5–7J); female with epigynum (entelegynes)	55	
52(51).	Eyes contiguous with AME surrounded by the others	Caponiidae (*Calponia*)	p. 122
52'.	Eyes not so arranged	53	
53(52').	Eyes in 3 groups, with AME forming a dyad and the others 2 triads (Figure 5–9F); chelicerae fused at base (Figure 5–9F)	Pholcidae (in part)	p. 123
53'.	Eyes in 2 transverse rows; chelicerae fused or not	54	
54(53').	Chelicerae fused at base; endites converging apically	Plectreuridae	p. 123
54'.	Chelicerae not fused; endites parallel	Tetragnathidae (in part)	p. 125
55(51').	Chelicerae fused at base (Figure 5–9F); eyes in 3 groups with AME forming a dyad and the others 2 triads (Figure 5–9F); legs long and slender, $PT/C > 1.6$, with flexible tarsi (*Note:* Although pholcids are haplogynes, some have complex genitalia and may be mistaken for entelegynes)	Pholcidae (in part)	p. 123
55'.	Chelicerae not fused; eyes not so arranged; legs usually shorter with rigid tarsi	56	
56(55').	Tarsi with at most a single trichobothrium	57	
56'.	Tarsi with 2 or more trichobothria (Figure 5–7C)	67	

57(56).	PLS with long apical segment, about as long as abdomen; eyes clustered on a mound at center of cephalon; Texas, Florida	**Hersiliidae (*Tama*)**	**p. 124**
57′.	PLS shorter; eye arrangement different; widespread in distribution	58	
58(57).	Anterior tibiae and metatarsi with prolateral row of curved spines in serrated series (Figure 5–7A)	Mimetidae	p. 125
58′.	Anterior legs without such spines	59	
59(58′).	Tarsus IV with ventral comb of serrated bristles (sometimes not distinct, lacking in *Argyrodes*) (Figure 5–7B); legs usually lacking spines; chelicerae usually with basal extension; epigynum without scape	60	
59′.	Tarsus IV without ventral comb; legs with spines; chelicerae lacking basal extension; epigynum sometimes with scape	61	
60(59).	Labium with anterior margin thickened; endites parallel; male palpus with large basal paracymbium	Nesticidae (in part)	p. 126
60′.	Labium with anterior margin unmodified; endites converging apically; male palpus with paracymbium inconspicuous or represented by an apical or ectal (outer) notch	**Theridiidae (in part)**	**p. 125**
61(59′).	Tarsi as long as or longer than metatarsi; tiny spiders, < 2 mm	62	
61′.	Tarsi shorter than metatarsi; size usually > 2 mm	63	
62(61).	Pedicel originating from opening on posterior slope of carapace; male abdomen with scutum; male metatarsus I without clasping spur; female without palpi	**Anapidae (*Gertschanapis*)**	**p. 125**
62′.	Pedicel origin below edge of carapace; male abdomen without scutum; male metatarsus I usually with clasping spur; female with palpi	Mysmenidae	p. 125
63(61′).	Sternum with a pair of pits at labial margin; tibia IV with long trichobothria; legs stout; size < 2.5 mm	Theridiosomatidae (*Theridiosoma*)	p. 125
63′.	Sternum without such pits; tibia IV without long trichobothria; legs variable; size usually larger	64	
64(63′).	Clypeus higher than 4 diameters of AME; chelicerae usually with stridulatory file on lateral surface, lacking condyle (Figure 5–7G); legs weakly spined; tarsi cylindrical; leg break at patella–tibia joint; sheet web builders	65	
64′.	Clypeus lower than 3 diameters of AME; chelicerae without stridulatory file, usually with condyle (Figure 5–7H); legs with strong spines; tarsi tapering distally; no leg break at patella–tibia joint; orb web builders	66	
65(64).	Male cymbium with integral retrolateral paracymbium; cymbium usually with a retromedian process armed with spines or cuspules; female epigynum forming stout, tonguelike projection with apical openings; size > 5 mm	**Pimoidae (*Pimoa*)**	**p. 126**
65′.	Male cymbium with retrolateral paracymbium attached by membrane (Figure 5–7J); cymbium usually lacking retromedian process, if present lacks spines or cuspules; female epigynum variable; size usually < 5 mm	**Linyphiidae (in part)**	**p. 126**
66(64′).	Endites square or rectangular; epigynum usually 3-dimensional, usually with scape, a central fingerlike projection, flat in *Hypsosinga*, *Mastophora*, and *Zygiella*; palpal tibia cup-shaped with irregular distal margin (except in *Zygiella*); builders of vertical orb webs	Araneidae	p. 125
66′.	Endites elongate, widest at distal edge; epigynum absent or a flat plate with at most a swelling (*Meta*) or pointed (*Metleucauge*); palpal tibia conical; builders of horizontal orb webs (except *Nephila*)	**Tetragnathidae (in part)**	**p. 125**

67(56').	Tarsal and metatarsal trichobothria in dorsal row, increasing in length distally (Figure 5–7C); at least anterior trochanters not notched	68	
67'.	Tarsal and metatarsal trichobothria in 2 irregular rows; all trochanters with shallow to deep notches	78	
68(67).	ALS enlarged, others reduced; clypeus high; endites strongly converging, lacking serrula	Zodariidae	p. 126
68'.	ALS at most only slightly larger than the others; endites not strongly converging; serrula present	69	
69(68').	Colulus large and broad, occupying at least half the width of the spinning area	70	
69'.	Colulus width less than ½ of the spinning area	71	
70(69).	Distribution: southern Florida	Desidae (*Paratheuma*)	p. 126
70'.	Distribution: southern California	Dictynidae (*Saltonia*)	p. 126
71(69').	Spinnerets arranged in transverse row; tracheal spiracle positioned well anterior of spinnerets	Hahniidae (in part)	p. 126
71'.	Spinneret arrangement not so modified; tracheal spiracle near spinnerets	72	
72(71').	Legs with plumose hairs; both eye rows strongly procurved, straight in *Tegenaria*, which has distinctive sternum markings	Agelenidae	p. 126
72'.	Legs lacking plumose hairs; eye rows straight; sternum typically 1 color	73	
73(72').	ALS contiguous or nearly so, thicker and usually longer than PLS	Cybaeidae (in part)	p. 126
73'.	ALS distinctly separated, shorter than PLS	74	
74(73').	Anterior tibia with 4 or more pairs of ventral spines	Hahniidae (in part)	p. 126
74'.	Anterior tibia with 3 or fewer pairs of ventral spines	75	
75(74').	Retromargin of chelicera with 2–5 equal-sized teeth, no denticles	76	
75'.	Retromargin of chelicera with both teeth and denticles or with more than 5 teeth	77	
76(75).	Size > 5 mm	Amaurobiidae (in part)	p. 126
76'.	Size < 5 mm	Hahniidae (in part)	p. 126
77(75').	Legs long and slender, PT/C > 1.25; male palp with apically produced cymbium	Hahniidae (*Calymmaria*)	p. 126
77'.	Legs shorter and stouter, PT/C < 1; male palp with unmodified cymbium	Dictynidae (in part)	p. 126
78(67').	Tarsi long and flexible	Trechaleidae (*Trechalea*)	p. 127
78'.	Tarsi not flexible	79	
79(78').	Clypeus high; AME small, others larger, forming hexagon (PER procurved) (Figure 5–9A); cheliceral margins with at most a single tooth; trochanters with shallow notches	Oxyopidae	p. 127
79'.	Clypeus low; PER recurved; chelicerae strongly toothed; trochanters deeply notched	80	
80(79').	PER strongly recurved with PLE posterior to PME so that eyes appear as 3 rows (Figure 5–9C); male palp lacking retrolateral tibial apophysis	Lycosidae	p. 127
80'.	PER not as strongly recurved, PLE lateral to PME (Figure 5–9D); male palp with retrolateral tibial apophysis	Pisauridae	p. 127
81(13').	Legs laterigrade: extending laterally from the body and twisted so that the morphologically prolateral surface of the anterior legs is functionally dorsal (Figure 5–11C)	82	
81'.	Legs prograde: anterior pair directed forward, posterior pair backward (Figure 5–11D)	85	

82(81).	Anterior legs thicker and longer than posterior ones (Figure 5–11C); tarsi lacking scopulae; chelicerae lacking teeth (except *Isaloides*)	**Thomisidae**	p. 128
82′.	Anterior legs not so enlarged, although leg II may be significantly longer than the others; tarsi with scopulae; chelicerae with teeth or denticles	83	
83(82′).	Smaller spiders (size $<$ 10 mm); cheliceral retromargin lacking teeth	**Philodromidae (in part)**	p. 128
83′.	Larger spiders (size usually $>$ 10 mm); cheliceral retromargin with teeth or denticles	84	
84(83′).	Metatarsi with dorsoapical trilobed membrane permitting hyperextension of tarsi (Figure 5–7F); tarsi with thick claw tufts; cheliceral retromargin with teeth; trochanters with deep notches, if not notched, then cheliceral retromargin with denticles, not teeth (*Pseudosparianthis*); southwestern United States and Florida	**Sparasiidae (in part)**	p. 128
84′.	Metatarsi lacking dorsoapical trilobed membrane; tarsi lacking claw tufts, but tarsal scopulae apically produced and may give the impression of tufts; cheliceral retromargin with teeth; trochanters with shallow notches; Arizona, New Mexico	**Tengellidae (*Lauricius*)**	p. 126
85(81′).	AME greatly enlarged, PER on lateral edge of carapace; carapace anteriorly truncate, face nearly vertical (Figure 5–9B)	**Salticidae**	p. 128
85′.	Eyes and carapace not so modified	86	
86(85′).	PER strongly recurved, eyes appear as 3 rows with anterior edge of PLE at or behind the posterior edge of PME	87	
86′.	PER variable, but not strongly recurved	90	
87(86).	Anterior tibia with at least 5 pairs of strong ventral spines	88	
87′.	Anterior tibia with fewer ventral spines	89	
88(87).	AER strongly recurved with ALE small and contiguous with PME and PLE; size $>$ 6 mm	**Ctenidae**	p. 128
88′.	AER straight to slightly recurved; size $<$ 6 mm	**Zoridae (*Zora*)**	p. 128
89(87′).	Carapace narrow, longer than wide; grass spiders; widespread in distribution	**Philodromidae (*Tibellus*)**	p. 128
89′.	Carapace broad, as long as wide; ground spiders; southern California to Arizona	**Homalonychidae (*Homalonychus*)**	p. 128
90(86′).	Tracheal spiracle at middle of abdomen; claw tufts of broad, lamelliform setae	**Anyphaenidae**	p. 128
90′.	Tracheal spiracle near spinnerets; claw tufts of normal setae	91	
91(90′).	ALS cylindrical, noticeably separated (may appear contiguous in *Micaria* and some *Orodrassus*) (Figure 5–8B); PME usually modified, either elliptical, oval or triangular; cheliceral margins usually weakly toothed, with only denticles, or lacking armature, sometimes keeled or with only 2–3 teeth; endites usually with distinct oblique median depression (not conspicuous in *Callilepis*); claw tufts always present	92	
91′.	ALS conical, contiguous at base (Figure 5–8A, C); PME usually round, if oval then anterior tibiae with 5–6 pairs of ventral spines; cheliceral margins strongly toothed; endites nearly parallel, often widened distally, usually lacking transverse median depression (if so, then anterior tibiae with 5–6 pairs of ventral spines); claw tufts present or absent	93	
92(91).	PER straight or recurved, rarely procurved (*Scopoides*); ALS with few moderately elongated spigots; tarsal claws and at least cheliceral promargin toothed	**Gnaphosidae (in part)**	p. 128
92′.	PER strongly procurved; ALS with numerous conspicuously elongated spigots; tarsal claws and cheliceral margins lacking teeth	**Prodidomidae (in part)**	p. 128

93(91′).	PLS distinctly 2-segmented, distal segment conical (Figure 5–8A)	Miturgidae	p. 127
93′.	PLS 1-segmented or, if 2-segmented, distal segment rounded	94	
94(93′).	Legs lacking spines, but anterior tibiae with ventral cusps	Corinnidae (Trachelinae)	p. 128
94′.	Legs with spines	95	
95(94′).	Anterior tibiae with more than 4 pairs of ventral spines	96	
95′.	Anterior tibiae with fewer than 4 pairs of ventral spines	98	
96(95).	Margin of sternum with triangular processes pointing toward coxae (precoxal triangles); trochanters with at most shallow notches	Corinnidae (Corinninae, Phrurolithinae)	p. 128
96′.	Precoxal triangles absent; trochanters deeply notched	97	
97(96′).	Size > 5 mm; tarsi not pseudosegmented	Tengellidae (in part)	p. 126
97′.	Size < 4 mm; tarsi pseudosegmented, posterior ones bent	Liocranidae (*Apostenus*)	p. 128
98(95′).	Abdomen of adults with scutum, covering entire abdomen of male and only anterior portion of female	Corinnidae (Castianeirinae)	p. 128
98′.	Abdomen of adult without scutum	99	
99(98′).	Endites concave ectally; precoxal triangles present (see couplet 96)	Clubionidae	p. 127
99′.	Endites straight or convex ectally; precoxal triangles usually absent, present in *Hesperocranum*, which has a distinctive dense brush of paired ventral bristles on anterior tibiae and metatarsi	Liocranidae (in part)	p. 128

Infraorder Mygalomorphae

These are the tarantulas and their allies. These spiders have large and powerful chelicerae with the fangs parallel to each other and two pairs of book lungs (Figure 5–6C). Females are long-lived and molt after sexual maturity. Most species are large (5–34 mm), heavy-bodied, and stout-legged. Many species are burrowers; some close their burrows with a trapdoor or silk collar. This group is largely tropical, but 138 species occur in North America. Most of these occur in the South and Southwest, but a few occur as far north as Massachusetts and southeastern Alaska.

Family **Antrodiaetidae—Folding-Door Spiders:** Members of this group have one to three dorsal abdominal tergites, some separation between the labium and the sternum, and a longitudinal or pitlike thoracic furrow. The burrows of these spiders are closed with a pair of flexible, silken doors (*Antrodiaetus*) or with a single thin door (*Aliatypus*), or remain open on a turret (*Atypoides*). They are medium-sized mygalomorphs (6–16 mm) with 25 species widely distributed in North America.

Family **Atypidae—Purse-Web Spiders:** These moderately large spiders (8–30 mm) have one dorsal abdominal tergite, sometimes enlarged into a scutum in males. The sternum and labium are fused, and the thoracic furrow is transverse. These spiders build silken tubes that may lie horizontally on the ground or extend up the base of a tree. The tubes are camouflaged with debris. If an insect comes in contact with the tube, the spider may bite through, grab the insect, and pull it through the tube. Eight species occur in the eastern United States, extending as far north as Wisconsin and New England.

Family **Mecicobothriidae:** Members of this group have one or two dorsal abdominal tergites; long, flexible, posterior spinnerets; a longitudinal thoracic furrow; and separation between the sternum and labium. They build webs consisting of sheets and tubes under debris. They are small to medium-sized mygalomorphs (4–18 mm) with six species known from western North America.

Family **Dipluridae:** Members of this group lack abdominal tergites and have very long posterior spinnerets. They may build a sheet web with a funnel, or a silk tube. This family includes the Appalachian species *Microhexura montivaga* Crosby and Bishop, which is on the endangered species list because of habitat destruction associated with the invasive balsam woolly adelgid (Hemiptera: Adelgidae). At 4 mm, *Microhexura montivaga* is the smallest mygalomorph in North America. Five species are known from North America.

Family **Ctenizidae:** Spiders in the families Ctenizidae and Cytraucheniidae are trapdoor spiders, constructing tunnels in the ground that are closed by a door hinged with silk. The door fits snugly and is usually well camouflaged. The tunnels may be simple or branched, and may even contain side chambers that are

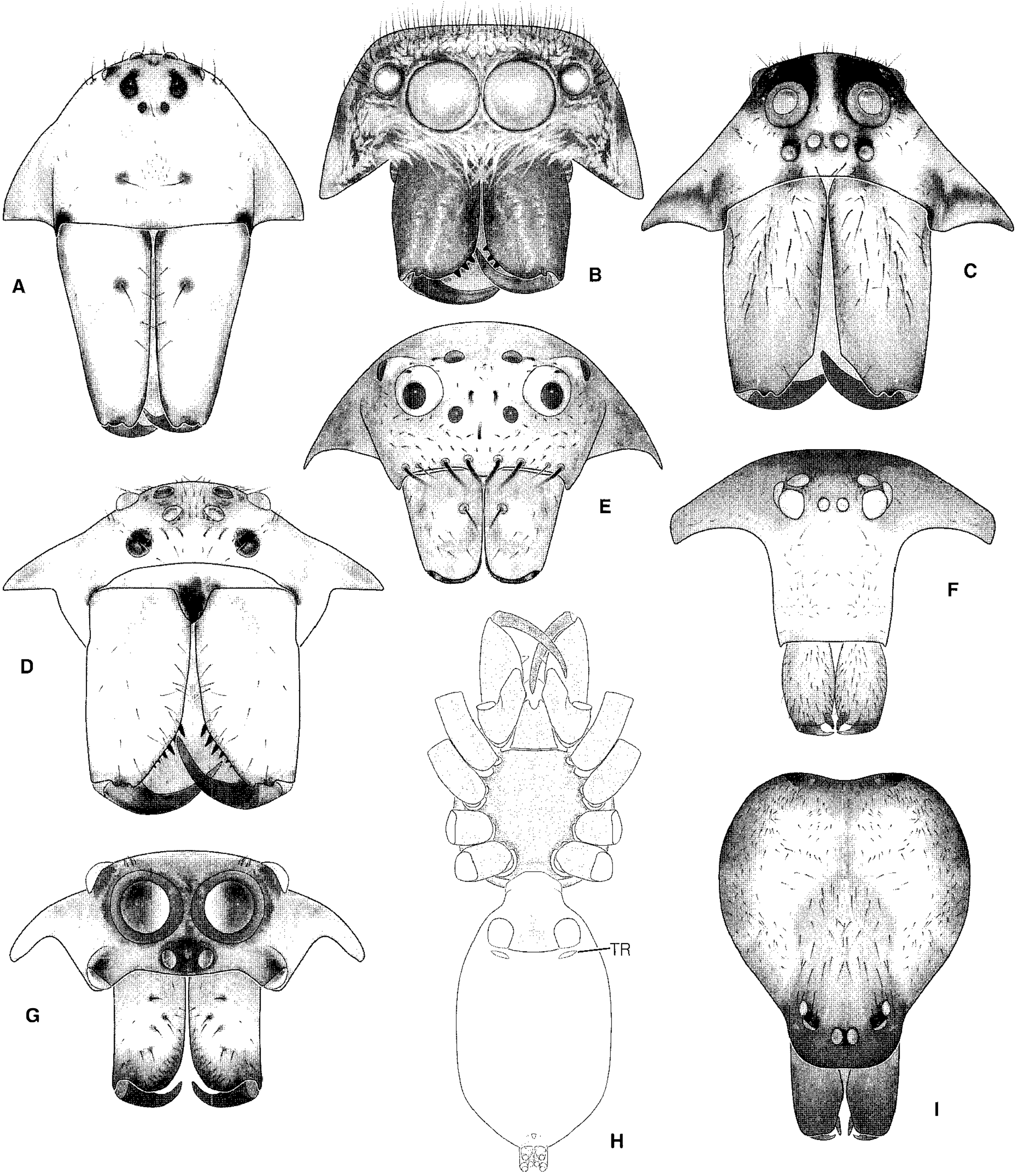


Figure 5–9 A–G, I, Eye arrangements of spiders; H, Ventral view. A, *Peucetia viridans* (Hentz) (Oxyopidae); B, *Salticus scenicus* (Clerck) (Salticidae); C, *Rabidosa rabida* (Walckenaer) (Lycosidae); D, *Pisaurina* sp. (Pisauridae); E, *Ozyptila pacifica* Banks (Thomisidae); F, *Pholcus phalangioides* (Fuesslin) (Pholcidae); G, *Deinopis spinosa* Marx (Deinopidae); H, *Dysdera crocata* C. L. Koch (Dysderidae); I, *Loxosceles reclusa* Gertsch and Mulaik (Sicariidae). *TR*, tracheal spiracle.

closed off from the main tunnel by hinged doors. These spiders can often be observed at night positioned at the entrance of a slightly opened door. When they detect prey passing close by, they rush out, capture the prey, and take it down into the tunnel. Ctenizids are distinguished by rows of short, stout spines on the first and second tarsi and metatarsi, and by the presence of a strongly procurved thoracic furrow. There are 15 species in the southern and western United States, including two members of the genus *Cyclocosmia*, which has the posterior part of the abdomen strongly truncated and covered in a heavily sclerotized disc. When the spider is inverted, the abdomen fits tightly against the walls of the burrow, forming a false bottom.

Family **Cyrtaucheniidae:** These trapdoor spiders (see preceding entry) have a transverse or slightly procurved thoracic furrow. Only the promargin of the chelicerae is toothed, although the retromargin may have a row of low, rounded tubercles. There are 17 species in the southern and western United States.

Family **Nemesiidae:** These spiders construct an open burrow that lacks a trapdoor. They are distinguished by a row of 4–7 stout setae on the upper inner surface of the chelicerae. There are five species in California.

Family **Theraphosidae—Tarantulas:** These distinctive, conspicuously hairy, two-clawed spiders are among the largest U.S. species (8–34 mm). They build open burrows, although these may be closed during the day by a thin sheet web or plugged with soil in the winter. Despite their reputation, the venom of North American tarantulas is not dangerous. However, they can produce clouds of urticating hairs by rubbing their abdomen with their hind legs. These hairs can irritate the mucous membranes of mammals, such as the eyes and respiratory passages. There are 57 species in the southwestern United States.

Infraorder Araneomorphae

This group contains the vast bulk of spider diversity. They differ from the Mygalomorphae in having the chelicerae hinged at the base to move in and out, rather than up and down as in mygalomorphs. They also have the fangs articulated so that they oppose each other, rather than moving in parallel (Figure 5–6B). The Araneomorphae are also united by the origin of the cribellum (Figure 5–8A), a specialized spinning organ apparently modified from the anterior median spinnerets. Most spiders have three functional pairs of spinnerets, although some mesotheles have nonfunctional remnants of this fourth pair. The cribellum has been lost multiple times in spider evolution. The Araneomorphae exclusive of Hypochilidae (and some of its non–North American relatives) forms the Araneoclada, which is united by the modification of the posterior pair of book lungs into a system of tracheae.

Family **Hypochilidae—Lampshade Spiders:** These cribellate, long-legged spiders are the only araneomorphs that retain the second pair of book lungs. The cribellum is undivided. North American species sit at the center of a circular mesh web, usually built on rock walls or the underside of overhanging ledges, often along streams. They are moderately large (8–12 mm), spindly spiders. There are 10 North American species in the Appalachians and Southwest.

Clade Haplogynae

The term *haplogyne condition* refers to the female reproductive system in which sperm is deposited and expelled via the same passages (contrast with Entelegynae). This condition is primitive for spiders, being found in mesotheles, mygalomorphs, and hypochilids. However, the grouping of the Haplogynae is supported as monophyletic by other lines of evidence, including the fusion of parts of the male palp to form a pyriform bulb (Figure 5–7I) and details of the spinnerets (Platnick et al. 1991). The Haplogynae include the next 13 families listed.

Family **Filistatidae:** These small to medium-sized spiders (3–15 mm) have the eight eyes tightly grouped on a rounded hump, a nearly horizontal clypeus, weak chelicerae fused medially, spinnerets and anal tubercle advanced from the posterior part of the abdomen to a ventral position, and a divided cribellum. They are the only araneomorph spiders in which the female molts after sexual maturity. They build sheet webs with radiating lines and a central funnel-shaped retreat. There are seven species in the southern and western United States.

Family **Caponiidae:** This family includes our only two-eyed spiders, although the number of eyes is variable. The lateral face of the chelicera has a stridulatory file. These small spiders (2–6 mm) lack book lungs, having the anterior and posterior respiratory organs modified into tracheae. Eight species are described from the southwestern United States. They live in litter and under stones.

Family **Dysderidae:** This family is represented in the United States by one introduced species, *Dysdera crocata* C. L. Koch. This two-clawed, ecribellate species has six eyes arranged in a tight cluster and very large, distally projecting chelicerae. The coxae of the two anterior pairs of legs are longer and thinner than those of the two posterior pairs (Figure 5–9H). They can be further distinguished from other spider families except Segestriidae and Oonopidae by having paired tracheal openings located just posterior to the book lungs (Figure 5–9H). These spiders live under bark or stones, where they construct a silken retreat and prey on isopods.

***Family* Segestriidae:** These three-clawed, ecribellate spiders have six eyes arranged in three dyads. They are distinguished by having the third pair of legs directed anteriorly. The tracheal system is as in dysderids. Segistriids are widespread in the United States, with seven described species.

***Family* Oonopidae:** Tiny (1.5–3 mm) ecribellate, two-clawed spiders with six eyes arranged in a tight group. Many species have large sclerotized plates in various configurations covering parts of the abdomen. The tracheal system is as in dysderids. These spiders can be found in leaf litter or buildings; some species are saltatory. There are 24 North American species, mostly in the southern United States.

***Family* Pholcidae—Cellar Spiders:** Small to medium-sized (1.5–9 mm) ecribellate, three-clawed spiders with fused chelicerae, six or eight eyes (Figure 5–9F), and very long, thin legs with tarsi subdivided into many pseudosegments. Unlike most haplogynes, the female genital region may be covered by a sclerotized "epigynum," as in most entelegyne spiders. However, the ducts of pholcid genitalia are haplogyne. Pholcids build irregular webs and may vibrate their webs when disturbed. Eggs are carried in the chelicerae loosely bound with silk. Pholcids are common in basements, garages, and other such unimproved structures. Thirty-four species are represented in North America.

***Family* Diguetidae:** Small to medium-sized (4–10 mm) ecribellate, three-clawed spiders with six eyes arranged in three dyads, long thin legs, and first tarsus of the male subdivided into many pseudosegments. The chelicerae are fused medially with a flexible membrane; the outer surface has a stridulatory file. A pair of tracheal spiracles are located anterior to the spinnerets about one third the distance to the epigastric furrow. These spiders live in silken tubes attached to a series of overlapping silken disks that are arranged like shingles on a roof and attached to vegetation. There are seven species in the southwestern United States.

***Family* Plectreuridae:** Medium-sized (5.5–12 mm) ecribellate, three-clawed spiders with eight eyes. The chelicerae are as in diguetids. These spiders construct silk tubes with silk radiating out at the entrance and are often found in hot, arid habitats. There are 16 species in the southwestern United States.

***Family* Ochyroceratidae:** Tiny (1–2 mm), ecribellate, six-eyed, three-clawed spiders with long, thin legs. These spiders resemble pholcids but lack pseudosegmented tarsi. The chelicerae are free, although a median lamella is present. These spiders have a distinctive purplish coloration. One species is found in Florida.

***Family* Leptonetidae:** Tiny (1–3 mm), three-clawed spiders that may be six-eyed, four-eyed, or blind. Most six-eyed species have a posterior dyad set apart from an anterior row of four eyes. There are 34 species, mostly in the southern United States. Some live in caves; others are associated with rocks and leaf litter.

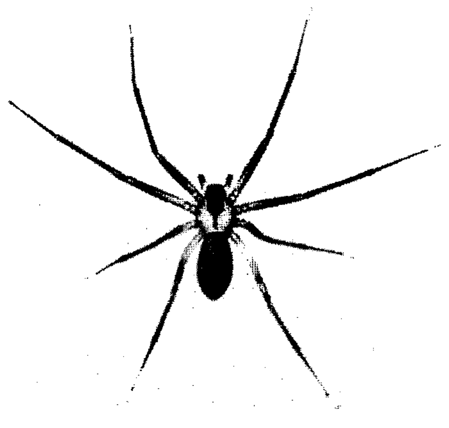
***Family* Telemidae:** Tiny (1–2 mm) three-clawed spiders that may be six-eyed or blind. Legs are long and thin. The book lungs are modified into an anterior set of tracheae. The abdomen has a distinctive sclerotized "zigzag" above the pedicel. There are four species in western North America, usually associated either with caves or damp leaf litter.

***Family* Sicariidae:** Small to medium-sized (5–12 mm) two-clawed spiders with six eyes arranged in three widely separated dyads (Figure 5–9I). The chelicerae are fused basally; the lateral face has coarse stridulatory striae. The legs are relatively long and slender. This family is represented in North America by the genus *Loxosceles*, which includes the brown recluse (Figure 5–10). *Loxosceles* contains some of the most poisonous species found in North America. Nevertheless, as mentioned, the frequency of envenomation has been exaggerated. Thirteen species of *Loxosceles* can be found in the Midwest, Southwest, and Atlantic seaboard.

***Family* Scytodidae—Spitting Spiders:** Small (3.5–5.5 mm), three-clawed spiders with six eyes arranged in three widely separated dyads, carapace domed in profile, highest posteriorly. The chelicerae are weak and fused basally. The legs are long and slender. These slow-moving spiders do not construct snares, but capture their prey by spitting out a mucilaginous substance that engulfs the prey and fastens it to the substrate. There are five North American species.

Clade Entelegynae

The term *entelegyne condition* refers to the female genitalia, which has separate ducts for the reception and expulsion of sperm. Entelegyne spiders usually have



U.S. Public Health Service

Figure 5–10 Brown recluse spider, *Loxosceles recluse* Gertsch and Mulaik. (Courtesy of U.S. Public Health Service).

the female genitalia covered by a sclerotized plate, the epigynum. The origin of the entelegyne condition is synapomorphic for a large group of spiders, but reversal to the "haplogyne" condition has occurred several times. Entelegyne spiders usually have a very complicated male pedipalp, featuring inflatable sacs and numerous sclerites. Prior to copulation, the sacs may fill with hemolymph, radically altering the configuration of the palpal bulb. The following spiders all belong to the Entelegynae.

Clade Eresoidea

This small group of spiders is mostly tropical and contains some social species. It includes cribellate and ecribellate spiders in three families, two of which are represented in North America.

Family **Oecobiidae:** This family of tiny (1–4.5 mm) three-clawed spiders is distinguished by its enlarged, jointed anal tubercle fringed with long curved hairs. Four eyes are well developed, four are degenerate. North American species have a divided cribellum, although other family members are ecribellate. This family is widely distributed and is often found in houses. There are eight North American species.

Family **Hersiliidae:** These flat, ecribellate three-clawed spiders are easily distinguished by their extremely long, tapered posterior spinnerets, with the distal segment about as long as the abdomen. Two species are, rarely, collected in southern Texas and Florida.

Clade Orbiculariae

This large group of three-clawed spiders includes the orb-weavers (Figure 5–11B) and their descendents. The Uloboridae and Deinopidae have an undivided cribellum and comprise the Deinopoidea; the 11 remaining families are ecribellate and belong to the Araneoidea. Many araneoids have a paracymbium attached to the retrolateral part of the cymbium (Figure 5–7J); this structure is of taxonomic importance.

Family **Uloboridae—Hackled-Band Orb-Weavers:** This four- or eight-eyed family lacks poison glands and builds a complete or reduced orb web. The family of small to medium-sized spiders (2–6 mm) is widespread in North America, with 14 species.

Family **Deinopidae—Ogre-Faced Spiders:** These night-active spiders are easily recognized by their extremely large posterior median eyes (Figure 5–9G). They have an elongate body (12–17 mm) and long,

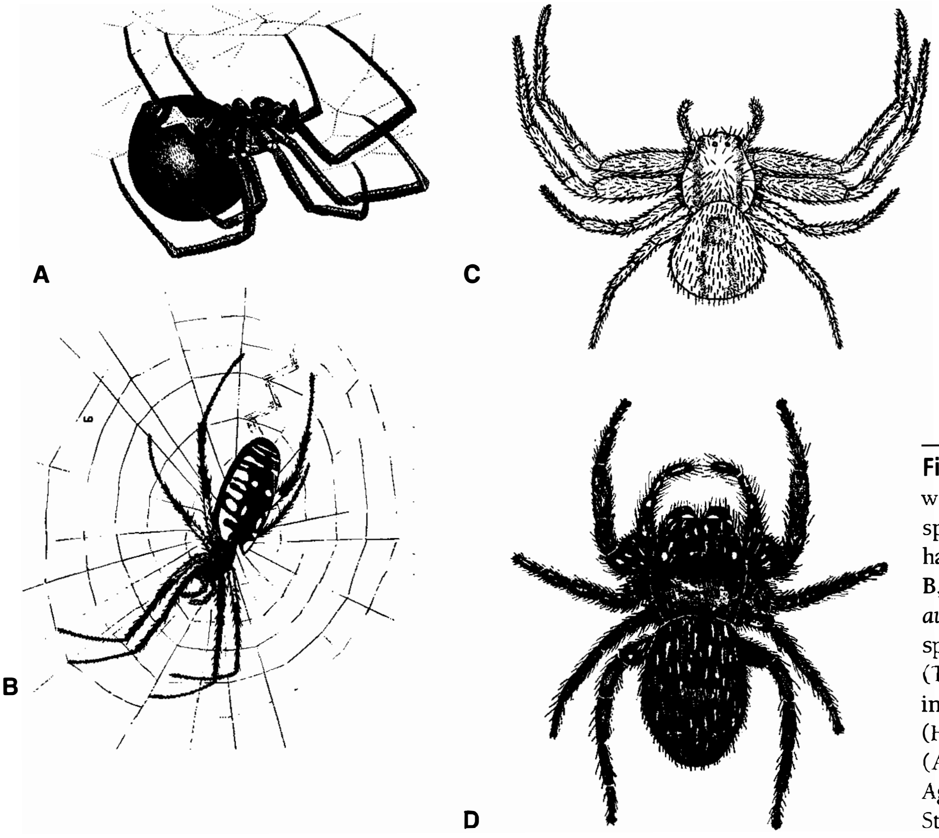


Figure 5–11 A, Black widow spider, *Latrodectus* sp. (Theridiidae), female hanging from its web; B, A garden spider, *Argiope aurantia* Lucas; C, A crab spider, *Misumenops* sp. (Thomisidae); D, A jumping spider, *Phidippus audax* (Hentz) (Salticidae). (A, Courtesy of Utah Agricultural Experiment Station.)

slender legs. They build a modified orb web, which they hold in their first two pairs of legs and cast like a net to capture prey. There is one species in the southeastern United States.

Family **Araneidae:** This is a diverse family, nearly all of which construct an orb web. Included in this group are the distinctive day-active spiny orb-weavers of the genera *Gasteracantha* and *Micrathena*, the garden spiders of the genus *Argiope*, and the Bolas spiders (genus *Mastophora*). Bolas spiders have abandoned the orb web; they use aggressive chemical mimicry to lure male moths, which they disable by striking them with a globule of sticky silk swung on the end of a line. There are 164 araneid species widely distributed in North America.

Family **Tetragnathidae:** This family of orb-weavers includes *Nephila clavipes* (L.), which builds a golden orb web that may be a meter in diameter. Female *Nephila* are very large (22–26 mm), but the males are much smaller (6–8 mm) and may be overlooked by collectors. *Nephila* can be common in the southern states. *Nephila* and most araneids build vertical orb webs; the remaining tetragnathids typically build horizontal orb webs. Members of the genus *Tetragnatha* often build webs over water. These spiders are long-bodied with very long and protruding chelicerae, especially in the males. There are 43 tetragnathid species widely distributed in North America.

Family **Theridiosomatidae:** These tiny (1–2.5 mm) orb-weavers are recognized by the presence of a pair of pits on the anterior part of the sternum adjacent to the labium, by their truncated sternum, and long trichobothria on tibiae III and IV. In our genus, the spider sits at the center of a vertical orb pulled into a cone by a thread emanating from the hub. There are two species in eastern North America.

Family **Symphytognathidae:** Symphytognathids and anapids both build small horizontal orb webs. These webs are distinctive because the spider builds a second series of radii after the sticky spiral is laid down. As a result, the spiral threads to not change direction at every radius, as they do in all other orb webs. Symphytognathid webs differ from anapid webs in having many more of these secondary radii, and by the absence of any radii outside the plane of the web (Eberhard 1982, 1986; Coddington 1986). Symphytognathids are distinguished by the basal fusion of their chelicerae, the absence of the female pedipalp (shared with Anapidae), the modification of the book lungs into tracheae, and the loss of the posterior tracheal system. There is one tiny (0.5 mm) four-eyed species in Florida.

Family **Anapidae:** Anapids are distinguished from other spiders by the presence of a spur arising from just above the oral cavity behind and between the chelicerae. The U.S. anapid species is a tiny (1–1.3 mm) eight-eyed spider found in Oregon and California. The book lungs are modified into tracheae, and the posterior tracheal system is lost (variable within the family). The abdomen of the male has a dorsal scutum; the female has the dorsal surface of the abdomen coriaceous and lacks a pedipalp.

Family **Mysmenidae:** These are minute (0.5–2 mm) eight-eyed spiders with soft abdomens. Females have a pedipalp. In most of our species, the male has a clasping spur on metatarsus I. The natural history of this group is diverse. Some build horizontal webs similar to those of anapids; others build a "three-dimensional" orb web, with radii not restricted to a single plane (Eberhard 1982, 1986; Coddington 1986); still others have abandoned web building to live as kleptoparasites in the webs of other spiders. Five species are widespread in North America.

Family **Mimetidae—Pirate Spiders:** Mimetids are characterized by a distinctive pattern of prolateral macrosetae on the first and second pair of legs (Figure 5–7A). These setae are arranged in a repeating pattern with each series containing several sequentially longer setae. Mimetids are araneophagous, aggressive mimics that typically invade the webs of other spiders. In the web, mimetid locomotion is typically very slow and characterized by frequent pauses. The mimetid then jerks or plucks the web, apparently imitating either a struggling insect or a courting male. When the victim moves close enough, the mimetid delivers a lethal bite of fast-acting venom (Bristowe 1958). The higher-level classification of mimetids is controversial.

Family **Theridiidae—Cobweb Spiders:** The following four families have abandoned the orb web in favor of a mesh sheet or three-dimensional cobweb. Theridiids typically build cobwebs, although some have adopted a kleptoparasitic lifestyle. They are usually eight-eyed (rarely six-eyed or blind) with a high clypeus; they may have a stridulatory organ above the pedicel between the carapace and abdomen. Theridiids usually have a comb of serrated setae on the fourth tarsus (Figure 5–7B). The tarsal comb is used to wrap prey in silk before envenomation. They rarely have teeth on the retrolateral margin of the chelicerae; teeth on the promargin occur but are also rare. The paracymbium, if present, is fused to the retrodistal part of the cymbium; the palpal tibia never has apophyses. The colulus is reduced or absent in some theridiids. This family includes the widow spiders (*Latrodectus*; Figure 5–11A), known for their potent venom (see earlier section on medically important spiders). Also represented among the 250 or so North American theridiid species are social spiders (*Anelosimus*) and kleptoparasites (*Argyrodes*).

Family **Nesticidae:** Nesticids may have eight, six, or four eyes or lack them altogether. They are typically pale in color and many species are associated with caves. Nesticids share several characteristics with theridiids, including a comb on tarsus IV; nesticids have a well-developed colulus. Males are readily distinguished from theridiids by presence of a conspicuous paracymbium fused to the retrobasal part of the cymbium. There are 37 species in North America, mostly endemic to the Appalachian region.

Family **Linyphiidae:** Linyphiids are the most species-rich spider family in North America (>800 species). Whereas some species build conspicuous sheet or dome-shaped webs, most species are tiny (1–3 mm) and live in leaf litter. The males of some species have bizarre head modifications that are associated with mating. Linyphiids are typically eight-eyed spiders (rarely six-eyed or blind) with a high clypeus, stridulatory striae on the lateral face of the chelicerae (Figure 5–7G), and a tendency for legs to break at the patella–tibia joint. The male palp features a small, often hooklike paracymbium attached to the retrobasal part of the cymbium by a membrane (Figure 5–7J). The palpal tibia may or may not have one or more apophyses.

Family **Pimoidae:** These spiders resemble linyphiids but are larger than most of those species (4.5–10.5 mm). They share with linyphiids a high clypeus, stridulatory striae, and leg breakage at the patella–tibia joint; they are best separated from them by details of the genitalia. The pimoid paracymbium is fused to the retrobasal part of the cymbium; the palpal tibia never has an apophysis. Thirteen species are represented in western North America.

The remaining spiders all belong to a large clade of spiders that, along with some non–North American groups, is the sister group to the Orbiculariae. This group does not have a formal taxonomic name at this time. Relationships among the taxa within this clade are not all well defined, but some distinctive groups are noted.

Family **Titanoecidae:** Small to medium-sized spiders (3.5–8 mm) with a well-developed, divided cribellum. These spiders sometimes have short, inconspicuous tarsal trichobothria. Males have ventral rows of short macrosetae on metatarsi and tibiae I and II, reduced in females. Four species are widespread in North America.

RTA (retrolateral tibial apophysis) clade

This large group of spiders all have a retrolateral apophysis on the male palpal tibia and have trichobothria on the tarsi, usually increasing in length distally (Figure 5–7C). Some families have two rows of trichobothria or an irregular cluster; others have the trichobothria secondarily reduced or lost. Lycosids have lost the retrolateral tibial apophysis.

Family **Dictynidae:** Dictynids are eight-eyed (occasionally six-eyed or blind), three-clawed spiders. The family includes both cribellate and ecribellate members; when present, the cribellum is usually entire, but occasionally is divided. Some dictynids have lost the tarsal trichobothria. There are over 280 North American species.

Family **Zodariidae:** These three-clawed, ecribellate spiders are distinguished by the absence of serrula on the distal margin of the endites, and by the reduction or absence of the posterior lateral and posterior median spinnerets. There are five North American species.

Family **Hahniidae:** Hahniids are ecribellate, three-clawed, sheet web builders. Many North American hahniids are easily distinguished by the configuration of the spinnerets in a transverse row and the advanced position of the tracheal spiracle. Other hahniids lack these characters, but are distinguished by rows of ventral spines on metatarsus and tibia I, by the presence of an undivided colulus, and the absence of plumose hairs.

Family **Agelenidae:** These three-clawed spiders are characterized by the presence of a divided colulus (Figure 5–8B). They typically have feathery hairs on the abdomen, elongated posterior spinnerets, and build a funnel web. Their webs can be quite numerous and conspicuous. There are 89 North American species.

Family **Cybaeidae:** These three-clawed spiders have contiguous anterior spinnerets that are longer than the posterior spinnerets and a more or less transverse, entire colulus. There are 44 North American species.

Family **Desidae:** These three-clawed spiders are characterized by their greatly enlarged, distally projecting chelicerae. We have only two species in North America. *Paratheuma* is a three-clawed, ecribellate spider with widely separated anterior spinnerets. It is associated with intertidal habitats in coastal Florida. *Badumna* has a divided cribellum and is introduced to California.

Family **Amphinectidae:** These three-clawed spiders have a divided cribellum and 5–7 strong teeth on both cheliceral margins. The male palpus has a filiform embolus enclosed in a membranous conductor. One species is introduced to California and the Gulf coastal region.

Family **Amaurobiidae:** Amaurobiids are three-clawed, cribellate or ecribellate spiders. They may build large sheet webs, or live in silk tubes with only a few lines radiating from the opening. There are 124 North American species.

Family **Tengellidae:** North American species are ecribellate spiders with two or three claws, claw tufts, and two rows of tarsal trichobothria. There are 23 North American species, including several associated with caves.

***Family* Zorocratidae:** These large (5–13 mm) spiders have a large, divided cribellum, scopulate tarsi, and two rows of tarsal trichobothria. Tarsus I has three claws; other tarsi have third claw absent. The chelicerae have lateral stridulatory striae. There are five species in the southwestern United States.

Superfamily Lycosoidea

The Lycosoidea includes the seven families listed next. The primitive condition for this group is that of a cribellate web builder. With the exception of one lycosid in the southeastern United States and an introduced species of zoropsid, all North American members of this group are ecribellate wandering hunters. This group is united by specializations of the eyes and characteristics of the male genitalia. Most members have three tarsal claws, but there are exceptions.

***Family* Ctenidae—Wandering Spiders:** These medium to large (6.5–30) spiders are recognized by their eye arrangement in which tiny anterior lateral eyes are almost contiguous with both the posterior median and posterior lateral eyes. They have two claws and claw tufts; scopulae vary from absent to dense and extending onto the metatarsi. Tarsal trichobothria are scattered, not in a defined row. This group is chiefly tropical; seven species occur in the southern United States.

***Family* Zoropsidae:** These two-clawed spiders have 6–7 pairs of ventral spines on the anterior tibiae; a calamistrum consisting of an oval patch, rather than one or two rows of setae; and a divided cribellum. A single species has been introduced to California.

***Family* Miturgidae:** These ecribellate, two-clawed spiders have dense scopulae and claw tufts. The posterior spinnerets are distinctly two-segmented and the distal segment is conical (Figure 5–8A). The absence of a thoracic furrow is indicative of *Cheiracanthium*, a miturgid genus of minor medical importance. There are 10 species in North America.

***Family* Oxyopidae—Lynx Spiders:** These three-clawed spiders can be recognized by the eye arrangement, with the anterior lateral and posterior pairs of eyes forming a hexagon, and the anterior median eyes below the anterior laterals (Figure 5–9A). The abdomen often tapers to a point posteriorly, the legs have many long macrosetae, and the tarsi have two rows of trichobothria; some are a distinctive bright green. Most lynx spiders forage over foliage and ambush their prey; others sit and wait on limbs or twigs. Members of the genus *Oxyopes* are strong jumpers. North American species do not construct a web or retreat, although web-building species can be found in the tropics. Eighteen species occur in North America.

***Family* Pisauridae—Nursery-Web and Fishing Spiders:** These medium to large (6.5–31 mm) spiders resemble wolf spiders, but differ in the eye arrangement: The anterior eye row is variable, usually smaller than the posteriors; the posterior row is strongly recurved, with the eyes subequal in size (Figure 5–9D). The egg sac is carried by the female under her cephalothorax, held there by the chelicerae and pedipalps. Before the eggs hatch, the female attaches the sac to a plant, builds a web around it, and stands guard nearby. Pisaurids forage for their prey and build webs only for their young. Some spiders in this group, particularly the fishing spiders of the genus *Dolomedes*, are quite large. *Dolomedes* live near water; they may walk over the surface of the water or dive beneath it to feed on aquatic insects and sometimes small fish. There are 13 species in North America.

***Family* Trechaleidae:** Large (14–16 mm), flattened, fast-moving, three-clawed spiders with long, flexible tarsi. There is one species in the Arizona, found near permanent streams in xeric regions. Females may carry a disc-shaped egg case attached to the spinnerets.

***Family* Lycosidae—Wolf Spiders:** Lycosids are distinctive three-clawed spiders recognized by their eye pattern: anterior eyes small in a more or less straight row; posterior median eyes very large, posterior lateral eyes smaller, positioned well behind the posterior medians (Figure 5–9C). The male palp lacks a tibial apophysis. Most North American species are foragers, except *Sosippus*, which constructs a sheet web with a funnel-shaped retreat. The egg sac is carried by the female, attached to her spinnerets. When the young hatch, they are carried for a time on the back of the female. Lycosids are widely distributed, with over 250 species in North America. They occur in many different habitats and are often quite common.

Clade Dionycha

The Dionycha include the 13 families listed next. This is a large group of two-clawed, eight-eyed (North American fauna), ecribellate spiders; it is probably not monophyletic. Unless otherwise noted, they have scopulae (at least on tarsi I and II, often on the metatarsi also) and claw tufts. All North American representatives forage without a web, although this does not hold true worldwide. Sparassidae, Selenopidae, Philodromidae, and Thomisidae are crab spiders with laterigrade legs (Figure 5–10C); the remaining families have the typical prograde orientation. Laterigrade legs are rotated so that the morphologically prolateral surface is dorsal.

***Family* Clubionidae:** These small to medium (2.5–10.5 mm) spiders have dense claw tufts and thin scopulae. They are usually pale yellow or light gray. Clubionids typically spend the day in silk tube retreats and forage for prey at night. There are 61 species in North America.

Family **Anyphaenidae:** These spiders resemble clubionids, but have the tracheal spiracle advanced at least half way between the spinnerets and the epigastric furrow, and the hairs of the claw tufts are somewhat flattened. Tarsus and metatarsus I and II have sparse scopulae. Their behavior is similar to clubionids, retreating to silk tubes by day and foraging at night. There are 39 species in North America.

Family **Corinnidae:** The legs usually have numerous ventral macrosetae (absent in *Trachelas*), dense claw tufts, and sparse scopulae. The abdomen often has sclerotized plates. Some species are ant mimics. North America has 122 species..

Family **Liocranidae:** These spiders typically lack paired ventral macrosetae on tibiae and metatarsi I and II; scopulae and claw tufts are absent or very thin. The abdomen often has iridescent setae or one or more scuta. There are eight species in North America.

Family **Zoridae:** These small to medium-size (2.5–7 mm) spiders have the anterior eye row nearly straight and the posterior eye row strongly recurved. The tibiae have 6–8 pairs of overlapping macrosetae. There are two species in North America.

Family **Gnaphosidae:** These spiders have the posterior median eyes flattened and irregularly shaped. The anterior spinnerets are cylindrical, sclerotized, and separated by at least their width (Figure 5–8B). The endites usually have an oblique depression on the ventral surface. These spiders are usually dark, but some have light markings on the abdomen. The males sometimes have a dorsal scutum. Unlike prodidomids, gnaphosids have teeth on the tarsal claws and at least the promargin of the chelicerae toothed. These spiders are typically active at night. Over 250 species are in North America.

Family **Prodidomidae:** These spiders are closely related to gnaphodids, but are distinguished in having the posterior eye row strongly procurved, both cheliceral and tarsal claw teeth are absent, and by details of the spinnerets. Two species live in the southern United States.

Family **Homalonychidae:** Moderately large (6.5–9 mm) spiders with strongly converging endites; they lack serrula on the anterior margin of the endites, teeth on the tarsal claws, and a colulus. Juveniles and adult females are usually covered with fine soil, which adheres to modified setae, providing effective camouflage. There are two species in the southwestern United States.

Family **Selenopidae:** These spiders have the one pair of posterior eyes advanced so that the anterior eye row appears to include six eyes; the posterior eye row includes two relatively large, widely spaced eyes. They are flattened, nocturnal, fast-moving, two-clawed spiders that lack a colulus. There are six species in the southern United States.

Family **Sparassidae—Giant Crab Spiders:** These large spiders (10–25 mm) are distinguished by a unique trilobed membrane on the dorsoapical part of the metatarsi (Figure 5–7F). Eleven species are generally confined to the southern United States, but are sometimes found in the North associated with shipments of bananas.

Family **Philodromidae:** These somewhat flattened spiders have dense scopulae and claw tufts. The eyes are usually subequal in size and not on tubercles. Teeth are present on the promargin of the chelicerae, absent from the retromargin. The legs are either subequal in length, or leg II is much longer than the others. There are nearly 100 species in North America.

Family **Thomisidae:** These somewhat flattened spiders lack scopulae and claw tufts. The lateral eyes are often larger than medians and positioned on tubercles (Figure 5–9E) The chelicerae are almost always without teeth, or have both margins toothed. Legs I and II are longer and thicker than legs III and IV (Figure 5–11C). One common species in this group is the goldenrod spider, *Misumena vatia* (Clerk), which is white or yellow with a red band on either side of the abdomen. This spider is a sit-and-wait predator, often occupying a flower and attacking pollinators. This spider can change color, over a period of a few days, depending on the color of the flower. There are over 140 species of thomisids in North America.

Family **Salticidae—Jumping Spiders:** These stout-bodied, short-legged spiders have a distinctive eye pattern, with the anterior median eyes by far the largest (Figures 5–9B, 5–11D). The body is rather hairy and is often brightly colored or iridescent. Some species are antlike in appearance. Jumping spiders forage for prey in the daytime. They approach their prey slowly, and then suddenly leap onto it. They can jump many times their own body length. Before jumping, they attach a silk thread dragline, which they can use to climb back to their starting position. Salticids are the world's most diverse spider family, with over 330 representatives in North America.

Order Ricinulei[14]—Ricinuleids

This is a small group of rare tropical arachnids. They are somewhat ticklike in appearance, and one of their distinctive features is a movable flap at the anterior end of the prosoma that extends over the chelicerae. The tarsi of the third pair of legs in the male are modified as copulatory organs. One species, *Cryptocellus dorotheae*

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[14] Ricinulei: *Ricin*, a kind of mite or tick; *ulei*, small (a diminutive suffix).

Gertsch and Mulaik, has been reported from the Rio Grande Valley of Texas. This arachnid is about 3 mm in length, is orange-red to brown in color, and occurs under objects on the ground. Some tropical species are larger (up to about 15 mm in length), and the majority have been taken in caves.

Order Opiliones[15]—Harvestmen, Daddy-Longlegs

These arachnids have the body rounded or oval, with the prosoma and opisthosoma broadly joined. There are usually two eyes, generally located on each side of a median elevation. Scent glands are present, their ducts opening to the outside above the first or second coxae. These glands secret a peculiar-smelling fluid when the animal is disturbed. Most species are predaceous or feed on dead animals or plant juices. The eggs are laid on the ground in the fall and hatch in the spring. Most species live a year or two. This order is divided into three suborders, the Cyphophthalmi, the Laniatores, and the Palpatores.

Suborder Cyphophthalmi—Mite Harvestmen

These are small, short-legged, mitelike forms, 3 mm in length or less, which differ from the other two suborders in having the scent glands opening on short conical processes. The eyes, if present, are far apart and indistinct. This group is represented in the United States by four species, which occur in the Southwest and the Far West.

Suborder Laniatores

This group is mainly tropical, but more than 60 species occur in the southern and western states, many of them in caves. These differ from the Palpatores in having the tarsi on the third and fourth legs with two or three claws (or one claw with three teeth). The pedipalps are large and robust, and their tarsi are armed with a strong claw. The legs are not unusually long.

Suborder Palpatores—Daddy-Longlegs

This group includes the harvestmen commonly called daddy-longlegs, which have very long and slender legs (Figure 5–12A). About 150 species occur in North America. These forms have the second pair of legs the longest, and the tarsi of all legs have just one claw. The pedipalps are smaller, their tarsi having a weak claw or none. Four families of this suborder occur in North America, but most U.S. species belong to the Phalangidae.

Order Acari[16]—Mites and Ticks

The Acari constitute a very large group of small to minute animals. More than 30,000 have been described, and it has been estimated that perhaps half a million more are still undescribed. The body is usually oval, with little (Figures 5–13, 5–14) or no (Figures 5–15 through 5–20) differentiation of the two body regions. Newly hatched young, called larvae, have only three pairs of legs (Figures 5–17B, 5–20A) and acquire the fourth pair after the first molt. A few mites have fewer than three pairs of legs (Figure 5–18). The instars between larva and adult are called *nymphs*.

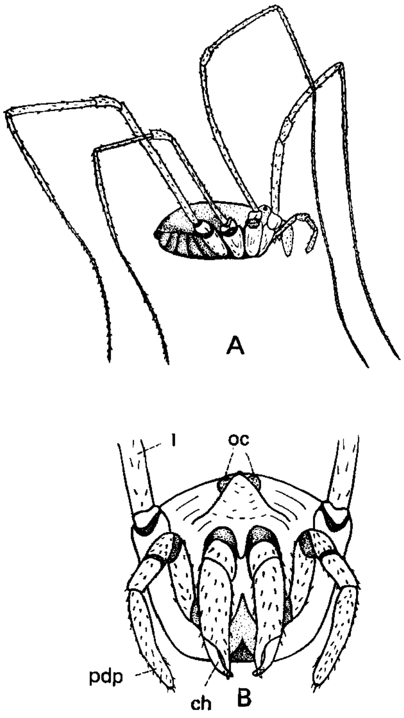

Figure 5–12 A harvestman or daddy-longlegs (Order Opiliones). A, Lateral view; B, Anterior view. *ch*, chelicera; *l*, front leg; *oc*, eyes or ocelli; *pdp*, pedipalp. The harvestmen typically have two eyes located on a tubercle, and the chelicerae are clawlike, as shown in B.

The Acari occur in practically all habitats in which any animal is found and rival the insects in their variations in habits and life histories. This group includes both aquatic and terrestrial forms, and the aquatic forms occur in both fresh and salt water. icari are abundant in soil and organic debris, where they usually outnumber other arthropods. Many are parasitic, at least during part of their life cycle, and both vertebrates and invertebrates (including insects) serve as hosts. Most of the parasitic forms are external parasites of their hosts. Many of the free-living forms are predaceous, and some of these prey on undesirable arthropods. Many are scavengers and help break down forest litter. Many are plant feeders, and some of these harm crops.

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[15] Opiliones: from the Latin, meaning a shepherd.

[16] Acari: from the Greek, meaning a mite.

Some of the parasitic forms are pests of humans and other animals, causing damage by their feeding and sometimes serving as vectors of disease. This group is of considerable biological and economic importance.

The groups of Acari have been variously arranged by different authorities; we follow here the arrangement of Barnes (1987), but call the three major groups of Acari "groups" rather than orders. This arrangement (with other spellings, names, or arrangements in parentheses) is as follows:

Order Acari—mites and ticks
  Group I. Opilioacariformes (Opilioacarida, Notostigmata; Parasitiformes in part)
  Group II. Parasitiformes
    Suborder Holothyrina (Holothyrida, Tetrastigmata)
    Suborder Mesostigmata (Gamasida)
    Suborder Ixodida (Ixodides, Metastigmata)—ticks
  Group III. Acariformes
    Suborder Prostigmata (Trombidiformes, Actinedida)
    Suborder Astigmata (Sarcoptiformes, Acaridida)
    Suborder Oribatida (Oribatei, Cryptostigmata)

Group I. Opilioacariformes

The members of this group (Figure 5–13) are elongate and somewhat leathery, and have the abdomen segmented. They are brightly colored and are superficially similar to some of the harvestmen (Opiliones). They are usually found under stones or in debris, and are omnivorous or predatory. The U.S. species occur in the Southwest.

Group II. Parasitiformes

These are medium-sized to large mites that have an unsegmented abdomen, and the tracheal system has ventrolateral spiracles.

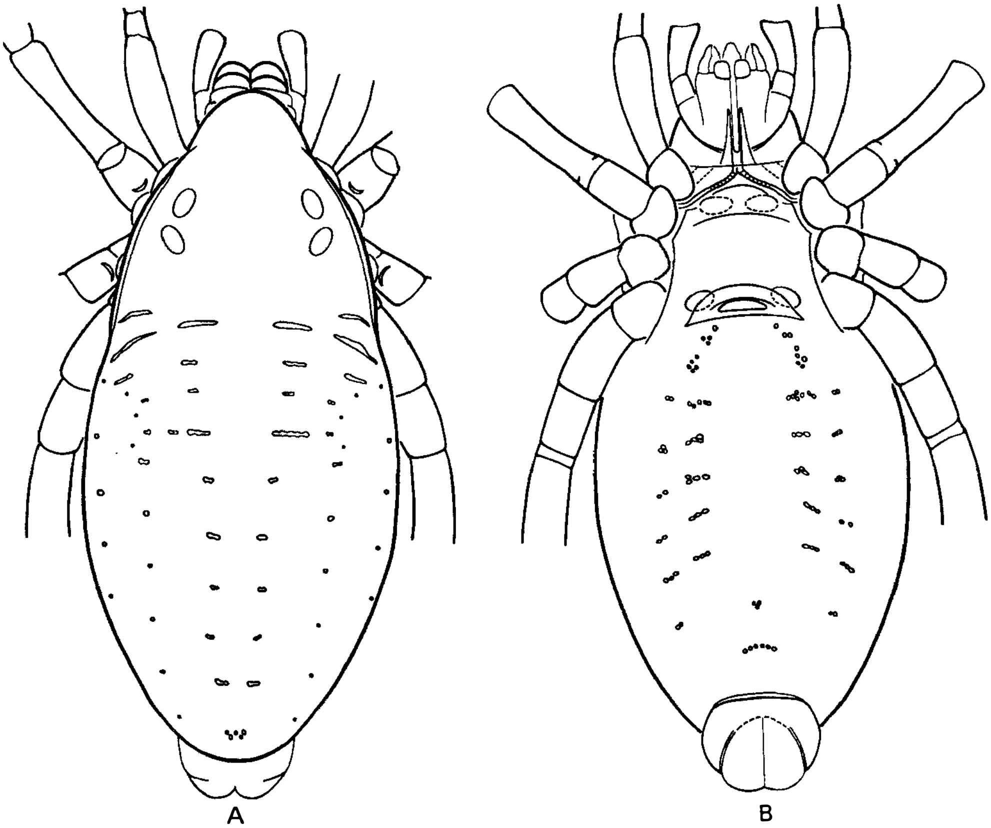

Figure 5–13 A female opilioacariform mite. A, Dorsal view; B, Ventral view. (From Johnston 1968, redrawn by van der Hammen.)

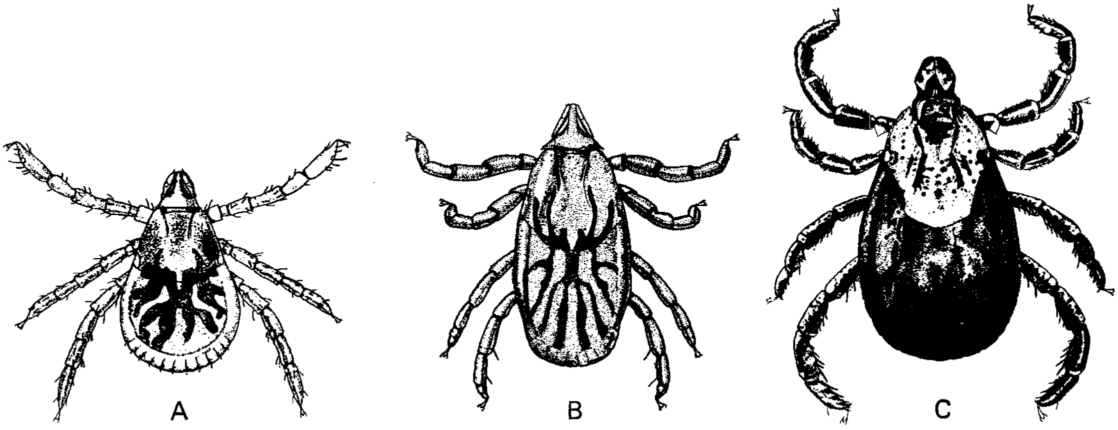

Figure 5–14 The American dog tick, *Dermacentor variabilis* (Say) (Ixodidae). A, Larva; B, Nymph; C, Adult (unengorged). (Courtesy of USDA.)

SUBORDER **Holothyrina**: The members of this group are fair-sized (2–7 mm in length), rounded or oval mites that occur in Australia, New Guinea, New Zealand, some islands in the Indian Ocean, and in the American tropics. They are found under stones or in decaying vegetation and are predaceous.

SUBORDER **Mesostigmata**: This is the largest suborder of the Parasitiformes and includes predaceous, scavenging, and parasitic forms. The majority are free-living and predaceous and are usually the dominant mites in leaf litter, humus, and soil. The parasitic mites in this group attack birds, bats, small mammals, snakes, insects, and rarely humans. One parasitic species, the chicken mite, *Dermanyssus gallinae* (De Geer), is a serious pest of poultry. It hides during the day and attacks poultry and sucks their blood at night. This species also causes a dermatitis in humans.

SUBORDER **Ixodida**—Ticks: Two families of ticks occur in North America, the Ixodidae or hard ticks and the Argasidae or soft ticks. Ticks are larger than most other Acari and are parasitic, feeding on the blood of mammals, birds, and reptiles. Those attacking humans are annoying pests, and some species serve as disease vectors. Ticks are the most important vectors of disease to domestic animals and second only to mosquitoes as vectors of disease to humankind. Certain ticks, especially engorging females feeding on the neck or near the base of the skull of their host, inject a venom that produces a paralysis; the paralysis may be fatal if the tick is not removed. The most important tick-borne diseases are Rocky Mountain spotted fever, relapsing fever, Lyme disease, tularemia, Texas cattle fever, and Colorado tick fever.

Ticks lay their eggs in various places, but not on the host; the young seek out a host after hatching. Most species have a three-host life cycle: the larva feeds upon one host, drops off, and molts; the nymph on a second; and the adult on a third. The hard ticks take only one blood meal in each of their three instars. They remain on the host for several days while feeding, but usually drop off to molt. The soft ticks generally hide in crevices during the day and feed on their hosts at night; each instar may feed several times. The hard ticks ordinarily have two or three hosts during their development, whereas the soft ticks may have many hosts. The cattle tick that transmits Texas cattle fever feeds on the same host individual during all three instars, and the protist that causes the disease is transmitted transovarially, that is, through the eggs to the tick's offspring. The hard ticks (Figure 5–14) possess a hard dorsal plate called the *scutum*, and they have the mouthparts protruding anteriorly and visible from above. The soft ticks (Figure 5–15) lack a scutum and

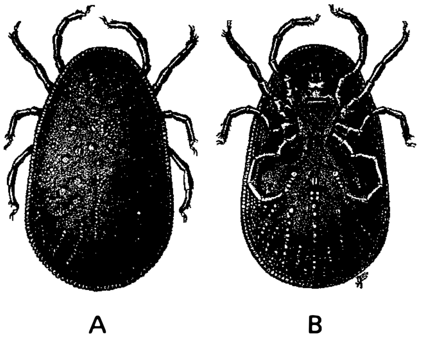

Figure 5–15 The fowl tick, *Argas persicus* (Oken), adult female (Argasidae). A, Dorsal view; B, Ventral view. (Courtesy of USDA.)

are soft-bodied, and the mouthparts are ventrally located and are not visible from above.

Group III. Acariformes

These are small mites that have the abdomen unsegmented, and the spiracles are near the mouth parts or absent (Figure 5–16).

SUBORDER **Prostigmata:** This is a large group whose members vary considerably in habits. Some are free-living (in litter, moss, or water) and vary in food habits; some are parasitic; and some are parasitic as larvae but predaceous as adults. This group includes the spider mites, gall mites, water mites, harvest mites, feather mites, and others.

The spider mites (Tetranychidae) are plant feeders, and some species do serious damage to orchard trees, field crops, and greenhouse plants. They feed on the foliage or fruits and attack a variety of plants. They are widely distributed, multivoltine, and sometimes occur in tremendous numbers. The eggs are laid on the plant and, during the warm days of summer, hatch in 4 or 5 days. There are four instars (Figure 5–17), and growth from egg to adult usually requires about three weeks. Most species overwinter in the egg stage. The immature instars are usually yellowish or pale in color, and the adults are yellowish or greenish. (These animals are sometimes called *red mites,* but they are seldom red.) Sex in these mites is determined by the fertilization of the egg. Males develop from unfertilized eggs, and females from fertilized eggs.

The gall mites (Eriophyoidea) are elongate and wormlike and have only two pairs of legs (Figure 5–18). A few species form small, pouchlike galls on leaves, but the majority feeds on leaves without forming galls and produces a rusting of the leaves. Some attack buds, and one forms the conspicuous witches'-broom twig gall on

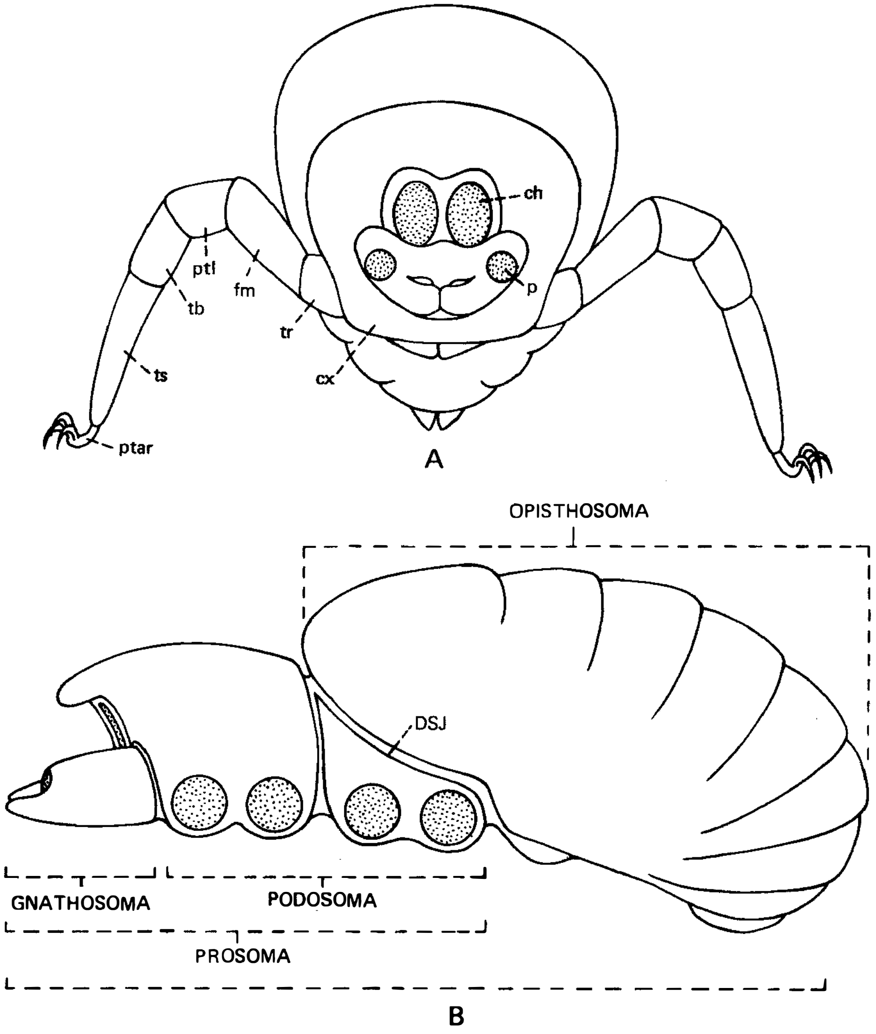

Figure 5–16 A generalized acariform mite. A, Anterior view; B, Lateral view. *ch*, socket of chelicera; *cx*, coxa; *DSJ*, disjugal furrow; *fm*, femur; *p*, socket of palp; *ptar*, pretarsus; *ptl*, genu or patella; *tb*, tibia; *tr*, trochanter; *ts*, tarsus. (Courtesy of Johnston.)

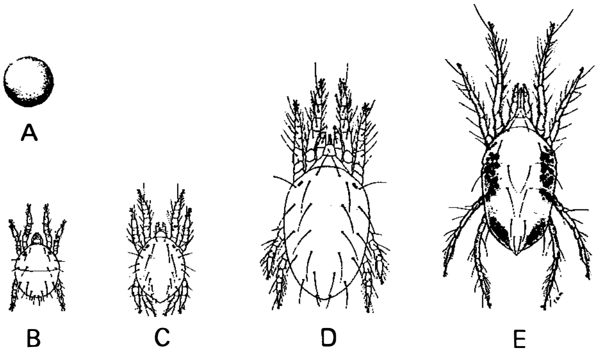

Figure 5–17 The fourspotted spider mite, *Tetranychus canadensis* (McGregor). A, Egg; B, First instar or larva; C, Second instar, or protonymph; D, Third instar, or deutonymph; E, Fourth instar, adult female. (Courtesy of USDA, after McGregor and McDunough.)

hackberry. Many gall mites are serious pests of orchard trees or other cultivated plants.

The water mites (Hydrachnidia, with 45 families in nine superfamilies) include a number of common and widely distributed freshwater species and a few marine forms. A few species occur in hot springs. The larvae are parasitic on aquatic insects, and most nymphs and adults are predaceous. Water mites are small, round-bodied, usually brightly colored (red or green), and often quite common in ponds. They crawl on the bottom and on aquatic vegetation and lay their eggs on the undersides of leaves or on aquatic animals (mainly freshwater mussels). Water mite larvae (mostly in the genus *Arrenurus*) are often abundant on the bodies of dragonflies and damselflies. They crawl from the nymph to the adult when the latter emerges and may remain there for a couple of weeks, feeding on the body fluids of the insect and eventually dropping off and developing into adults (if they happen to get into a suitable habitat).

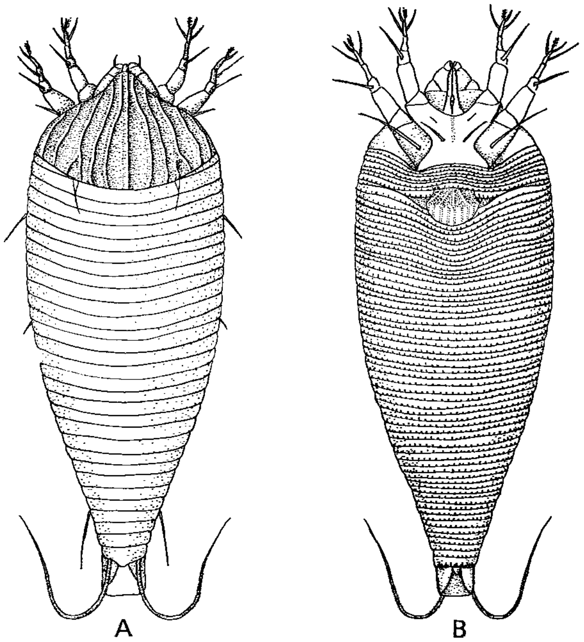

Figure 5–18 A gall mite, *Phyllocoptes variabilis* Hodgkiss, a species attacking sugar maple; 460×. A, Dorsal view; B, Ventral view. (Redrawn from Hodgkiss 1930.)

The harvest mites (also called *chiggers* or *redbugs*) (Trombiculidae) are ectoparasites of vertebrates in the larval stage, whereas the nymphs and adults are free-living and predaceous on small arthropods and arthropod eggs. Harvest mites lay their eggs among vegetation. On hatching, the larvae crawl over the vegetation and attach to a passing host. They insert their mouthparts into the outer layer of the skin, and their saliva partly digests the tissues beneath. The larvae remain on the host for a few days, feeding on tissue fluid and digested cellular material, and then drop off. These mites are small (Figure 5–19A) and are seldom noticed. Their bites, however, are quite irritating, and the itching persists for some time after the mites have left. On people, these mites seem to prefer areas where the clothing is tight. A person going into an area infested with chiggers can avoid being attacked by using a good repellent, such as dimethyl phthallate or diethyl toluamide. This material can be put on the clothing, or the clothing can be impregnated with it. A good material to reduce the itching caused by chiggers is tincture of benzyl benzoate. In Asia, the Southwest Pacific, and Australia, certain harvest mites serve as vectors of scrub typhus, or tsutsugamushi disease. This disease caused more than 7,000 casualties in the U.S. armed forces during World War II.

The feather mites (19 families, in the superfamilies Analgoidea, Pterolichoidea, and Freyanoidea) constitute a large group whose members occur on the feathers or skin or (rarely) in the respiratory system of birds. Many are found on particular feathers or feather areas of their hosts. They are seldom of economic importance, although they often occur in considerable numbers on poultry or avian pets. They appear to be scavengers, feeding on feather fragments and oily secretions on the feathers. Some of those occurring on aquatic birds feed on diatoms.

The Tarsonemidae is a large family of mites that includes species associated with insects or plants, and some cause human dermatitis. Some species live in the galleries of bark beetles, where they feed on the bark

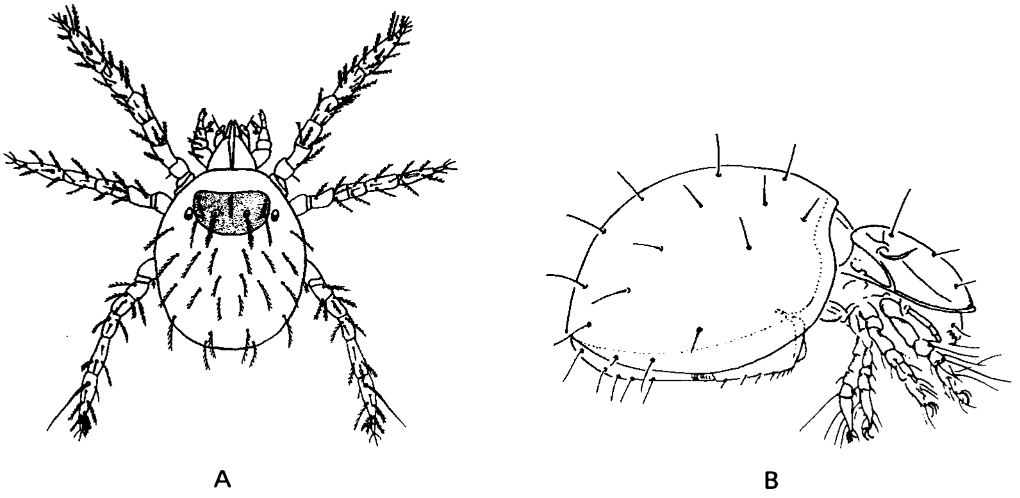

Figure 5–19 A, A chigger, the larva of *Eutrombicula alfreddugesi* (Oudemans), 215×; B, An oribatid mite (family Euphthiracaridae). (A, Redrawn from a US Public Health Service release; B, Courtesy of the Institute of Acarology).

beetle eggs. They are carried from gallery to gallery on the bodies of the beetles. Species in the genus *Acarapis* occur on the bodies of honey bees. *Acarapis woodi* (Rennie) causes what is known as Isle of Wight disease in honey bees. A few species (*Tarsonemus* and other genera) have been implicated in cases of human dermatitis.

SUBORDER Astigmata: The mites in this group are mostly terrestrial and nonpredatory. Some are parasitic, and a few of the parasitic forms are important pests of people and animals. The most important mites in this group are probably those that infest stored foods and those that cause dermatitis in humans and animals.

The Acaroidea are principally scavengers, occurring in animal nests, stored foods, and plant tissues. Those occurring in stored foods (cereals, dried meats, cheese, and the like) not only damage or contaminate these materials, but they may get on people and cause a dermatitis called *grocer's itch* or *miller's itch*.

The most important mites in this suborder that cause dermatitis in humans and animals are in the families Psoroptidae and Sarcoptidae. The Psoroptidae include the mange mites, which attack various animals (Figure 5–20), and the Sarcoptidae include the itch or scab mites. These mites burrow into the skin and cause severe irritation, and the resulting scratching often causes additional injury or leads to secondary infection. One of the best treatments for scabies (infection by these mites) is the application of a solution of benzyl benzoate. Species of *Dermatophagoides* (Pyroglyphidae) are common inhabitants of houses and have been implicated in house dust allergies.

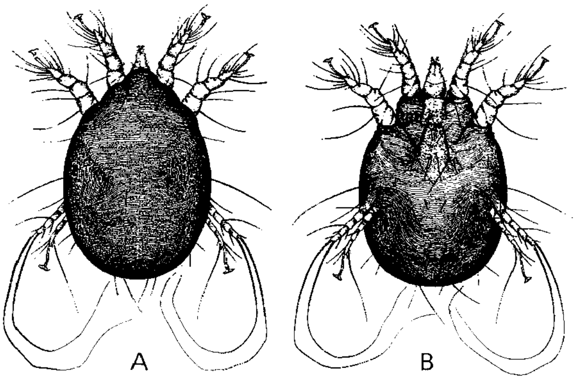

Figure 5–20 The sheep scab mite, *Psoroptes ovis* (Hering), female. A, Dorsal view; B, Ventral view. (Courtesy of USDA.)

SUBORDER Oribatida: This is a large group of small mites (0.2–1.3 mm) that vary considerably in form. Some superficially resemble small beetles (Figure 5–20B) and are called *beetle mites*. Some species have winglike lateral extensions of the notum. In a few cases these extensions, called *pteromorphs*, are hinged, contain "veins," and are provided with muscles. Oribatid mites are found in leaf litter, under bark and stones, and in the soil. They are mainly scavengers. They make up a large percentage of the soil fauna and are important in breaking down organic matter and promoting soil fertility. Some species of Oribatuloidea have been found to serve as the intermediate hosts of

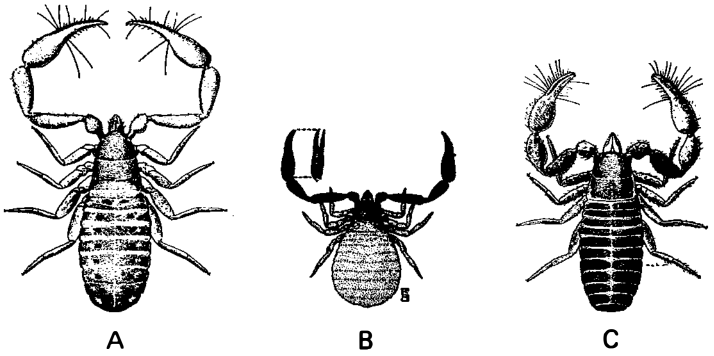

Figure 5–21 Pseudoscorpions. A, *Dactylochelifer copiosus* Hoff; B, *Larca granulata* (Banks); C, *Pselaphochernes parvus* Hoff. (Courtesy of Hoff and Illinois Natural History Survey.)

certain tapeworms that infest sheep, cattle, and other ruminants.

Order Pseudoscorpiones[17]—Pseudoscorpions

The pseudoscorpions are small arachnids, seldom more than 5 mm in length. They resemble true scorpions in having large chelate pedipalps, but the opisthosoma is short and oval, there is no sting (Figure 5–21), and the body is quite flat. The pseudoscorpions differ from most other arachnids in lacking a patellar segment in the legs. Eyes may be present or absent; if present, there are two or four, located at the anterior end of the prosoma.

The Pseudoscorpiones are a fair-sized group, with about 200 species in North America, and its members are common animals. They live under bark and stones, in leaf litter and moss, between the boards of buildings, and in similar situations. They sometimes cling to and are carried about by large insects. They feed chiefly on small insects, which they catch with their pedipalps. Most species have venom glands that open on the pedipalps. These animals have silk glands, the ducts from which open on the chelicerae.[18] The silk is used in making a cocoon in which the animal overwinters.

ORDER **Solifugae[19]—Windscorpions**: This is a fair-sized group of arachnids (about 120 species in North America) whose members occur chiefly in the arid or desert regions of the West (one species occurs in Florida). They are called by a variety of names: *windscorpions* (they run "like the wind"), *sunscorpions, sunspiders,* and *camelspiders.* They are 20–30 mm in length, are usually pale colored and somewhat hairy, and the body is slightly constricted in the middle (Figure 5–4C). One of their most distinctive features is their very large chelicerae (often as long as the prosoma), giving them a very ferocious appearance. They may bite, but they do not have venom glands. The males have a flagellum on the chelicera. The fourth legs bear, on the ventral side of the coxae and trochanters, five short, broad, T-shaped structures (attached by the base of the T) called *racket organs* or *malleoli,* which are probably sensory in function.

Windscorpions are largely nocturnal, hiding during the day under objects or in burrows. They are fast-running and predaceous, sometimes even capturing small lizards. The pedipalps and first legs are used as feelers, and these animals run on the last three pairs of legs. Two families occur in the United States, the Ammotrechidae (first legs without claws, and anterior edge of prosoma rounded or pointed) and the Eremobatidae (first legs with one or two claws, and anterior edge of prosoma straight).

Class Pycnogonida[20]—Sea Spiders

The pycnogonids are marine, spiderlike forms with long legs. They are occasionally found under stones near the low-tide mark, but usually occur in deep water. They are predaceous and have a sucking proboscis. The body consists principally of prosoma; the opisthosoma is very small. The sea spiders vary in length from

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[17] Pseudoscorpiones: *pseudo,* false; *scorpiones,* scorpion.

[18] Another name given to this order, Chelonethida, refers to this feature: *chelo,* claw; *neth,* spin.

[19] Solifugae: *sol,* sun; *fugae,* flee (referring to the nocturnal habits of these animals)

[20] Pycnogonida: *pycno,* thick or dense; *gonida,* offspring (referring to the eggs).

one to several centimeters. Little is known of their habits, because they are uncommon.

Collecting and Preserving Chelicerates

To obtain a large collection of chelicerates, one needs primarily to collect in as many different types of habitats as possible. Chelicerates are frequently very abundant, often as abundant as insects or more so. The general collector of insects is likely to encounter more spiders and mites than any other types of chelicerates; therefore, the following suggestions are concerned primarily with these groups.

Chelicerates occur in a great variety of situations and can often be collected with the same techniques and equipment used in collecting insects. Many can be taken by sweeping vegetation with an insect net. Many can be obtained with beating equipment, that is, using a sheet or beating umbrella beneath a tree or bush and beating the bush to knock off the specimens. The ground forms can be found running on the ground or under stones, boards, bark, or other objects. Many can be found in the angles of buildings and similar protected places. Many of the smaller forms can be found in debris, soil litter, or moss and are best collected by means of sifting equipment such as a Berlese funnel (Figure 35–5) or a screen sieve or by means of pitfall traps. Many are aquatic or semiaquatic and can be collected in marshy areas with aerial collecting equipment or in water with aquatic equipment. The parasitic species (various mites and ticks) usually must be looked for on their hosts.

Many chelicerates are nocturnal, and collecting at night may prove more successful than collecting during the day. Very few are attracted to lights, but they can be spotted at night with a flashlight or a headlamp. The eyes of many spiders reflect light, and with a little experience and a light, you can locate many spiders at night. Scorpions are fluorescent and can be collected at night with a portable ultraviolet light to make them visible.

Chelicerates should be preserved in fluids rather than on pins or points. Many forms, such as the spiders, are very soft-bodied and shrivel when dry. They are usually preserved in 70 to 80% alcohol. There should be plenty of alcohol in the bottle in relation to the specimen, and it is often desirable to change the alcohol after the first few days. Many workers preserve mites in Oudeman's fluid, which consists of 87 parts of 70% alcohol, 5 parts of glycerine, and 8 parts of glacial acetic acid. The chief advantage of this fluid is that the mites die with their appendages extended so that subsequent examination is easier. Alcohol is not suitable for preserving gall mites. Such mites are best collected by wrapping infested plant parts in soft tissue paper and allowing them to dry. This dried material can be kept indefinitely, and the mites may be recovered for study by warming the dried material in Kiefer's solution (50 grams of resorcinal, 20 grams of diglycolic acid, 25 milliliters of glycerol, enough iodine to produce the desired color, and about 10 milliliters of water). Specialists on mites prefer specimens in fluid, rather than mounted on permanent microscopic slides, so that all aspects and structure can be studied.

Chelicerates can be collected by means of a net, forceps, vial, or small brush, or by hand. For biting or stinging forms, it is safer to use some method other than collecting them with the fingers. Specimens collected with a net can be transferred directly to a vial of alcohol, or collected in an empty vial and later transferred to alcohol. Because some species are quite active, it is sometimes preferable to put them first into a cyanide bottle and transfer them to alcohol after they have been stunned and are quiet. Specimens collected from the ground or debris may be picked up with forceps or coaxed into a bottle; the smaller specimens (found in any situation) may be picked up with a small brush moistened with alcohol.

Spider webs that are flat and not too large can be collected and preserved between two pieces of glass. One piece of glass is pressed against the web (which will usually stick to the glass because of the viscous material on some of the silk strands), and then the other piece of glass is applied to the first. It is often desirable to have the two pieces of glass separated by thin strips of paper around the edge of the glass. Once the web is between the two pieces of glass, bind the glass edges together with binding tape. Spider webs are best photographed when covered with moisture (dew or fog) or dust. They can often be photographed dry if illuminated from the side and photographed against a dark background.

Subphylum Crustacea[21]—Crustaceans

The crustaceans are a large and varied group of arthropods, with more than 44,000 known species. Most of them are marine, but many occur in fresh water, and a few are terrestrial. In addition to the larger and more familiar types, such as lobsters, crayfish, (Figure 5–22) crabs, and shrimp, a multitude of small to minute aquatic forms are very important in aquatic food webs.

The appendages and body regions vary greatly in this group, but typically there are two pairs of antennae, the functional jaws consist of endite lobes of the gnathal (jaw) appendages, and many of the appendages are biramous. A

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[21] Crustacea: from the Latin, referring to the crustlike exoskeleton possessed by many of these animals.

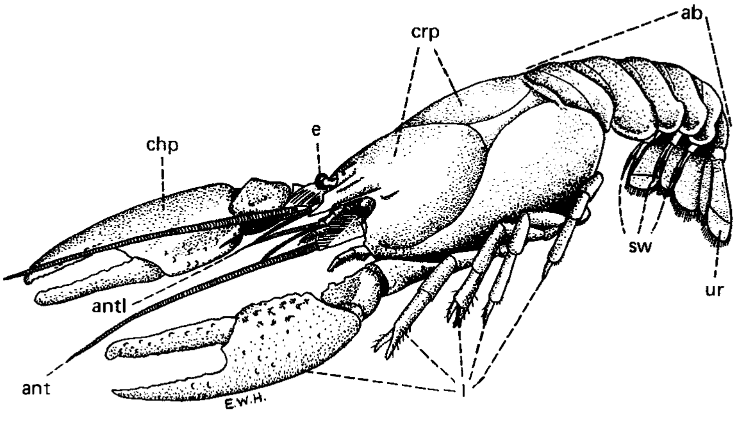

Figure 5–22 A crayfish (*Cambarus* sp.), natural size. *ab*, abdomen; *ant*, antenna; *antl*, antennule; *chp*, cheliped; *crp*, carapace; *e*, eye; *l*, legs (including cheliped); *sw*, swimmerets; *ur*, uropod.

biramous appendage bears a process at its base (arising from the second segment of the appendage) that is more or less leglike, giving the appendage a two-branched appearance (Figure 5–1C). There may be an exite lobe on the basal segment, as in trilobites, and in some cases this functions as a gill. There are differences in this group in the nature of the body regions. Sometimes there are two fairly distinct (and nearly equal-sized) body regions, the cephalothorax and the abdomen, with the cephalothorax bearing the antennae, gnathal appendages, and legs. Sometimes the abdominal appendages occupy only a small portion of the total body length. There is typically a terminal telson. The cephalothorax in many crustaceans is covered by a shieldlike portion on the body wall called the *carapace*. The abdomen lacks paired appendages except in the Malacostraca.

The smaller crustaceans, particularly those in the Branchiopoda, Copepoda, and Ostracoda, are abundant in both salt and fresh water. The chief importance of most species is that they are food for larger animals and thus are an important part in the food webs leading to fish and other larger aquatic animals. A few species are parasitic on fish and other animals, and the barnacles are often a nuisance when they encrust pilings, boat bottoms, and other surfaces. Many of the small crustaceans can be easily maintained in indoor aquaria and are frequently reared as food for other aquatic animals.

Class Branchiopoda[22]

Most members of class Branchiopoda occur in fresh water. Males are uncommon in many species, and parthenogensis is a common mode of reproduction. Both unisexual (parthenogenic) and bisexual reproduction occur in many species, and the factors controlling the production of males are not well understood.

There are differences of opinion regarding the classification of these crustaceans, but four fairly distinct groups are usually recognized, the Anostraca, Notostraca, Conchostraca, and Cladocera. The first two of these are sometimes placed in a group called the Phyllopoda, and the last two are sometimes called the Diplostraca.

The Anostraca,[23] or fairy shrimps (Figure 5–23A), have an elongated and distinctly segmented body, without a carapace and with 11 pairs of swimming legs, and the eyes are on stalks. The fairy shrimps are often abundant in temporary pools. The Notostraca,[24] or tadpole shrimps, have an oval convex carapace covering the anterior part of the body, 35 to 71 pairs of thoracic appendages, and two long, filamentous caudal appendages. These animals range in size from about 10 to 50 mm and live only in the western states. The Conchostraca,[25] or clam shrimps, have the body somewhat flattened laterally and entirely enclosed in a bivalved carapace and have 10 to 32 pairs of legs. Most species are 10 mm in length or less. The Cladocera,[26] or water fleas (Figure 5–24A), have a bivalved carapace, but the head is not enclosed in the carapace. There are four to six pairs of thoracic legs. The water fleas are 0.2 to 3.0 mm in length and are very common in freshwater pools.

Three groups of small crustaceans living in fresh water have a bivalved carapace, and observers are likely to confuse these groups. The Ostracoda (Figure 5–24B,C) and Conchostraca have the body completely enclosed in the carapace, whereas in the Cladocera (Figure 5–24A) the head is outside the carapace. The Ostracoda have only three pairs of thoracic legs; the Conchostraca have 10 to 32 pairs.

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[22] Branchiopoda: *branchio*, gill; *poda*, foot or appendage

[23] Anostraca: *an*, without; *ostraca*, shell.

[24] Notostraca; *not*, back; *ostraca*, shell.

[25] Conchostraca: *conch*, shell or shellfish; *ostraca*, shell.

[26] Cladocera: *clado*, branch; *cera*, horn (referring to the antennae).

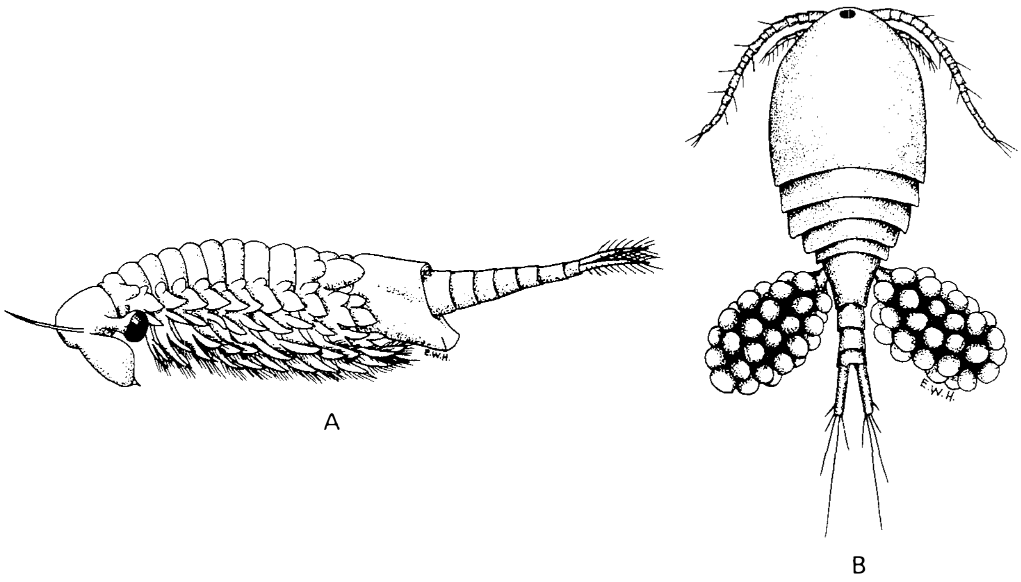

Figure 5–23 Crustaceans. A, A fairy shrimp, *Eubranchipus* (subclass Branchiopoda, order Anostraca), 6×; B, A female copepod, *Cyclops* sp., 50×, with two egg sacs at posterior end of body.

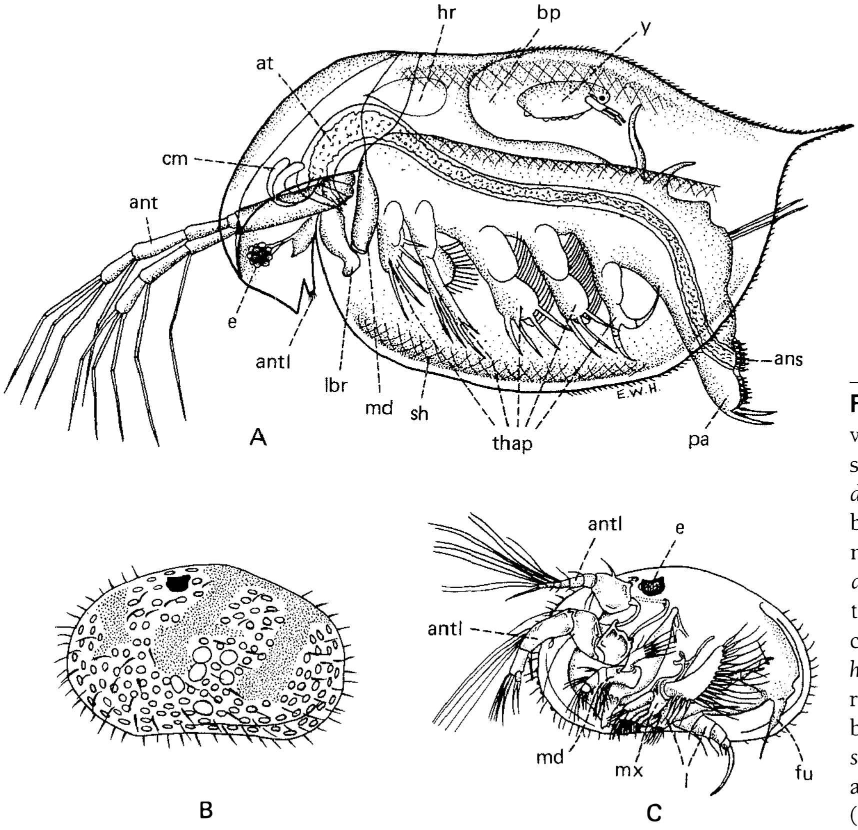

Figure 5–24 Crustaceans. A, A water flea or cladoceran, *Daphnia* sp., 25×; B, An ostracod, *Cypridopsis* sp., lateral view; C, Same, but with left valve of carapace removed. *ans*, anus; *ant*, antenna; *antl*, antennule; *at*, alimentary tract; *bp*, brood pouch; *cm*, caecum; *e*, compound eye; *fu*, furca; *hr*, heart; *l*, first and second thoracic legs; *lbr*, labrum; *md*, mandible; *mx*, maxilla; *pa*, postabdomen; *sh*, bivalved shell; *thap*, thoracic appendages; *y*, developing young. (C, Modified from Kesling.)

Class Copepoda[27]

Some of the copepods are free-swimming, and others are parasitic on fish. The parasitic forms are often peculiar in body form and quite unlike the free-swimming forms in general appearance. This group includes both marine and freshwater forms. The female of most copepods carries her eggs in two egg sacs located laterally near the end of the abdomen (Figure 5–23B). The parasitic copepods, often called *fish lice,* live on the gills or the skin or burrow into the flesh of their host. When numerous, they may seriously injure the host. Some species serve as intermediate hosts of certain human parasites for example, the fish tapeworm, *Diphyllobothrium latum* (L.).

Class Ostracoda[28]

The ostracods have a bivalved carapace that can be closed by a muscle, and when the valves are closed the animal looks like a miniature clam (Figure 5–24B,C). When the valves of the carapace are open, the appendages are protruded and propel the animal through the water. Many species are parthenogenic. Most of the ostracods are marine, but there are also many common freshwater species.

Class Cirripedia[29]

The best-known members of the class Cirripedia[29] are the barnacles, the adults of which live attached to rocks, pilings, seaweeds, boats, or marine animals, and which are enclosed in a calcareous shell. A few species are parasitic, usually on crabs or mollusks. Most members of this group are hermaphroditic; that is, each individual has both male and female organs. Some barnacles, such as the goose barnacle (Figure 5–25A), attach the shell to some object by a stalk. Others, such as the rock barnacle (Figure 5–25B), are sessile and do not have stalks.

The Smaller Crustacean Classes

Included in the smaller crustaceans are the classes Cephalocarida,[30] Mystacocarida,[31] Branchiura,[32] Tantulocarida,[33] and Remipedia.[34] The nine known species of Cephalocarida are marine bottom–dwelling forms that often occur in very deep water. The Mystacocarida are minute (mostly about 0.5 mm in length) marine forms living in the intertidal zone. Nine species of these have been described. The Branchiura are ectoparasites on the skin or in the gill cavities of fish (both marine and freshwater fish). About 130 species are known. The Tantulocarida (four known species) are ectoparasites of deep-water crustaceans. The Remipedia (eight known species) have a long and wormlike body, and live in island caves connected to the sea.

Class Malacostraca[35]

The Malacostraca, the largest of the crustacean classes, includes the larger and better known forms, such as the lobsters, crayfish, crabs, and shrimps. They differ from

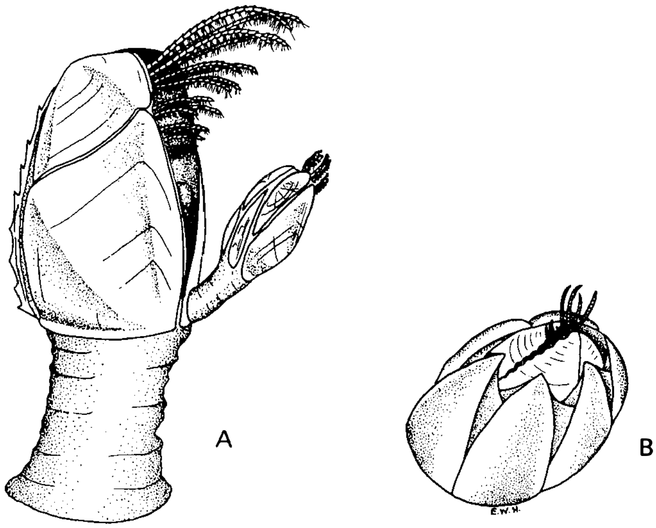

Figure 5–25 Barnacles. A, A goose barnacle, *Lepas* sp., 3×; **B**, A rock barnacle, *Balanus* sp., 2×. The basal stalk or peduncle of the goose barnacle is at the animal's posterior end; the biramous appendages protruding from the shell at the top of the figure are the posterior thoracic legs; a second small individual is shown attached to the first.

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[27] Copepoda: *cope*, oar; *poda*, foot or appendage.

[28] Ostracoda: from the Greek, meaning shell-like (referring to the clamlike character of the carapace).

[29] Cirripedia: *cirri*, a curl of hair; *pedia*, foot or appendage.

[30] Cephalocarida: *cephalo*, head; *carida*, a shrimp.

[31] Mystacocarida: *mystaco*, mustache; *carida*, a shrimp.

[32] Branchiura: *branchi*, gill; *ura*, tail.

[33] Tantulocarida: *tantula*, little; *carida*, a shrimp.

[34] Remipedia: *remi*, an oar; *pedia*, foot or appendage.

[35] Malacostraca: *malac*, soft; *ostraca*, shell.

the preceding classes (sometimes called the Entomostraca) in having appendages (swimmerets or pleopods) on the abdomen. There are typically 19 pairs of appendages, the first 13 being cephalothoracic and the last 6 abdominal. The leglike appendages on the cephalothorax are often chelate. This class contains some 13 orders. Only the more common ones can be mentioned here.

ORDER **Amphipoda:**[36] The body of an amphipod is elongate and more or less compressed; there is no carapace; and seven (rarely six) of the thoracic segments are distinct and bear leglike appendages. The abdominal segments are often more or less fused, and hence the six or seven thoracic segments make up most of the body length (Figure 5–26). This group contains both marine and freshwater forms. Many of them, such as the beach fleas (Figure 5–26B), live on the beach under stones or in decaying vegetation. Most amphipods are scavengers. Some tropical species are common on the floor of moist forests.

ORDER **Isopoda:**[37] The isopods are similar to the amphipods in lacking a carapace, but are dorsoventrally flattened. The last seven thoracic segments are distinct and bear leglike appendages. The abdominal segments are more or less fused, and hence the thoracic segments (with their seven pairs of legs) make up most of the body length (Figure 5–27). The anterior abdominal appendages of the aquatic forms usually bear gills. The terminal abdominal appendages are often enlarged and feelerlike. The isopods are small (most are less than 20 mm in length), and most are marine, but some live in fresh water and some are terrestrial. The marine forms generally live under stones or among seaweed, where they are scavengers or omnivores, but a few are wood-boring (apparently feeding chiefly on the fungi in the wood), and some are parasitic on fish or other crustaceans. The most common isopods away from the ocean are the sowbugs or woodlice—blackish, gray, or brownish animals usually found under stones, boards, or bark. Some sowbugs (often called *pillbugs*) can roll into a ball. In some areas sowbugs are important pests of cultivated plants.

ORDER **Stomatopoda**[38]**—Mantis Shrimps:** These are predaceous marine forms, mostly 5 to 36 cm in length, with the body dorsoventrally flattened. There are three pairs of legs, in front of which are five pairs of maxillipeds, the second of which is very large and chelate. A small carapace covers the body in front of the legs, and the abdomen is a little wider than the carapace. The mantis shrimps are often brightly colored: green, blue, red, or patterned. This group is principally tropical. U.S. species occur chiefly along the southern coasts.

ORDER **Decapoda:**[39] This order contains the largest and probably the best known of the crustaceans, the lobsters, crayfish (Figure 5–22), crabs (Figure 5–28), and shrimps. The carapace of a decapod covers the entire thorax. Five pairs of the cephalothoracic appendages are leglike, and the first pair of these usually bears a large claw. The abdomen may be well developed (lobsters and crayfish) or much reduced (crabs). This is a very important group, because many of its members are used as food, and their collection and distribution underpin a large coastal industry.

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[36] Amphipoda: *amphi*, on both sides, double; *poda*, foot or appendage.

[37] Isopoda: *iso*, equal; *poda*, foot or appendage.

[38] Stomatopoda: *stomato*, mouth; *poda*, foot or appendage.

[39] Decapoda: *deca*, ten; *poda*, foot or appendage.

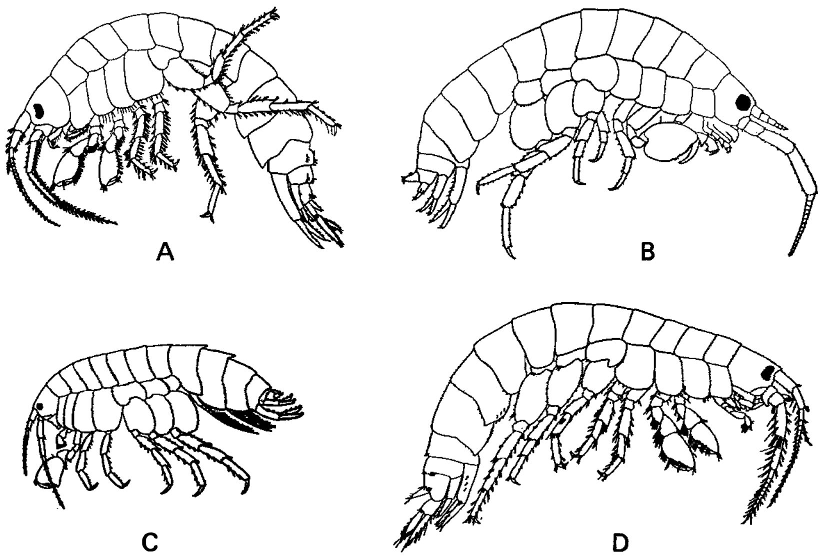

Figure 5–26 Amphipods. A, A common freshwater scud, *Dikerogammarus fasciatus* (Say), 10–15 mm in length; B, A sand flea or beach flea, *Orchestia agilis* Smith, abundant underneath seaweed along the coast near the high tide mark; C, A common freshwater scud, *Hyalella knickerbockeri* (Bate), about 7 mm in length; D, A sea scud, *Gammarus annulatus* Smith, a common coastal form, about 15 mm in length. (Courtesy of Kunkel and the Connecticut State Geology and Natural History Survey; C, After Smith.)

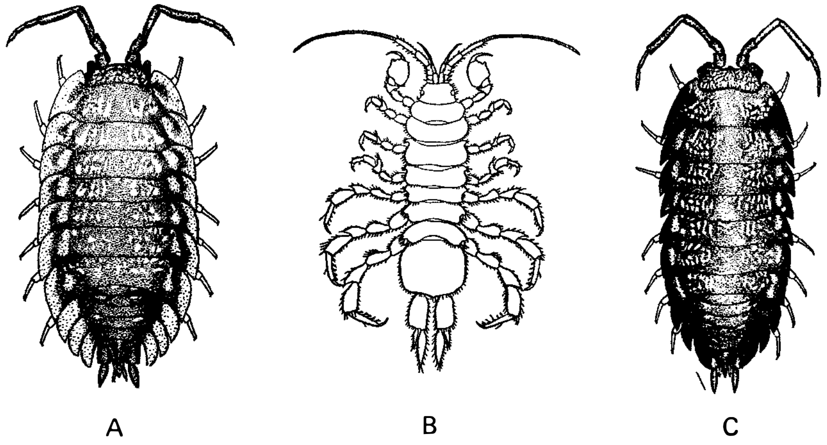

Figure 5–27 Isopods. A, *Oniscus asellus* L., a common sowbug; B, *Asellus communis* Say, a common freshwater isopod; C, *Cylisticus convexus* (DeGeer), a pillbug capable of rolling itself into a ball. (Courtesy of the Connecticut State Geology and Natural History Survey. A, C, Courtesy of Kunkel 1918, after Paulmier; B, Courtesy of Kunkel 1918, after Smith.)

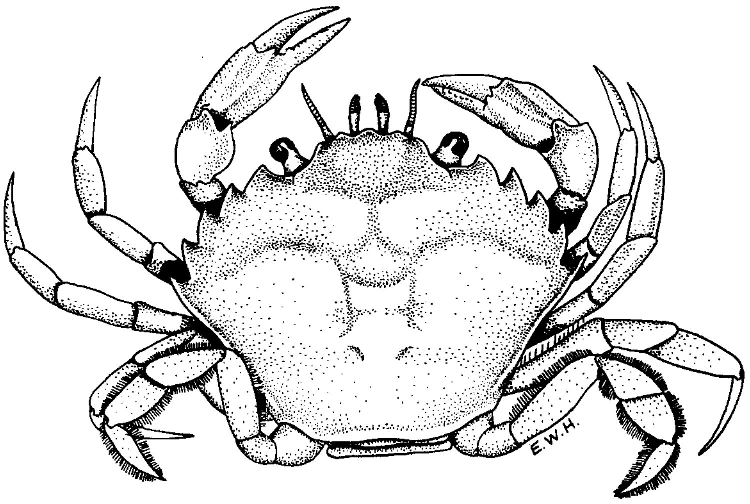

Figure 5–28 A green crab, *Carcinides* sp., 1½×.

Collecting and Preserving Crustacea

The aquatic crustaceans must be collected with various types of aquatic collecting equipment. Most can be collected by a dip net. A white enamel dipper is the best means of collecting many of the smaller forms. The dipper is simply dipped into the water, and any small animals in the dipper can be easily seen. Forms so collected can be removed by means of an eye dropper or (if fairly large) by forceps. The smaller forms in ponds, lakes, and the ocean are often collected in a fine-mesh *plankton net*, towed by a boat. Many larger forms are collected by traps. Such traps (or "pots") are the standard means of collecting lobsters and crabs. The shore-dwelling and terrestrial forms can be collected by hand or forceps or possibly (for example, beach fleas) with an aerial insect net. Handle the larger forms with well-developed claws with care, because the claw can inflict serious injury. The safest way to pick up a large crayfish or lobster is from above, grasping the animal at the back of the carapace.

To obtain a variety of Crustacea, collect in a variety of places. When collecting in water, investigate every possible aquatic niche. Some crustaceans are free-swimming; some burrow in bottom mud; some live under stones; and many are found on aquatic vegetation. The shore-dwelling forms are usually under stones, debris, or decaying vegetation along the shore.

Preserve crustaceans in fluids (for example, 70 to 95% alcohol). Most smaller forms must be mounted on microscope slides for detailed study. Some of the smaller Malacostraca can be preserved dry (for example, pinned), but specimens preserved in fluid are more satisfactory for study.

Subphylum Atelocerata[40]

The members of this subphylum have a single pair of antennae and uniramous (unbranched) appendages. According to Manton (1977), the mandibles of these species differ from those of Crustacea in that the entire appendage makes up the functional portion of the mandible (and not only the basal portion). She placed the groups included here (following) together with the Onychophora as the phylum Uniramia (concluding that the Arthropoda is a polyphyletic taxon). We believe this position has not been adequately supported. In terms of her conclusion regarding the structure of the mandible, both Crustacea and Hexapoda have similar expression patterns of the gene *distal-less*, falsifying the hypothesis that one (the crustacean mandible) is gnathobasic, whereas the other represents the entire appendage of the mandibular segment. Further, Manton's conclusion requires evidence that one or more taxa now classified as arthropods are more closely related to a nonarthropod group. Until such evidence is available, we continue to treat the Arthropoda as a monophyletic unit and do not consider the onychophorans to be arthropods.

Other than Onychophora, the Atelocerata includes the Myriapoda and Hexapoda. Recent molecular studies have done little to alleviate the considerable uncertainty concerning the interrelationships among Crustacea, Myriapoda, and Hexapoda. Some researchers suggest that the myriapods are a polyphyletic or paraphyletic group; others that hexapods are most closely related to a subset of crustaceans (and, therefore, that Crustacea is paraphyletic).

Class Diplopoda[41]—Millipedes. The millipedes are elongate, wormlike animals with many legs (Figure 5–29). Most millipedes have 30 or more pairs of legs, and most body segments bear 2 pairs. The body is cylindrical or slightly flattened, and the antennae are short and usually seven-segmented. The external openings of the reproductive system are located at the anterior end of the body, between the second and third pairs of legs. One or both pairs of legs on the seventh segment of the male are usually modified into gonopods, which function in copulation. Compound eyes are usually present. The first tergum behind the head is usually large and is called the *collum* (Figure 5–30A).

The head in most millipedes is convex above, with a large epistomal area, and flat beneath. The bases of the mandibles form a part of the side of the head. Beneath the mandibles, and forming the flat ventral surface of the head, is a characteristic liplike structure called the *gnathochilarium* (Figure 5–30B, gna). The gnathochilarium is usually divided by sutures into several areas: a median more or less triangular plate, the mentum (mn); two lateral lobes, the stipites (stp); two median distal plates, the laminae linguales (ll); and usually a median transverse basal sclerite, the prebasalare (pbs), and two small laterobasal sclerites, the cardines (cd). The size and shape of these areas differ among groups of millipedes, and the gnathochilarium often provides characters by which the groups are recognized.

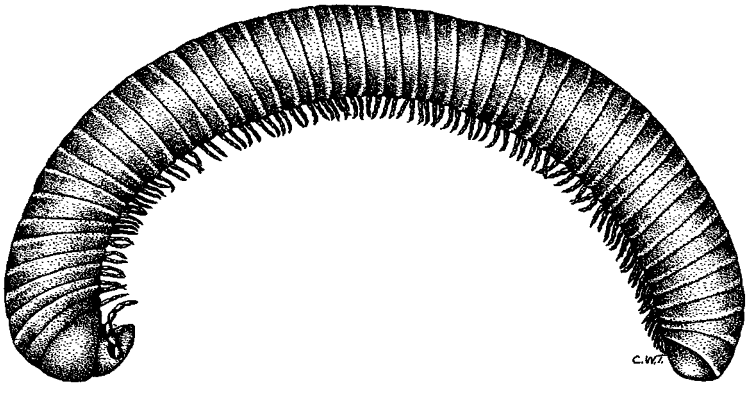

Figure 5–29 A common millipede, *Narceus* sp. (order Spirobolida), 1½×.

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[40] Atelocerata: *atelos*, defective; *keras*, horn; referring to the fact that the second antennae are present in these taxa only as embryonic rudiments.

[41] Diplopoda: *diplo*, two; *poda*, foot or appendage (referring to the fact that most body segments bear two pairs of legs).

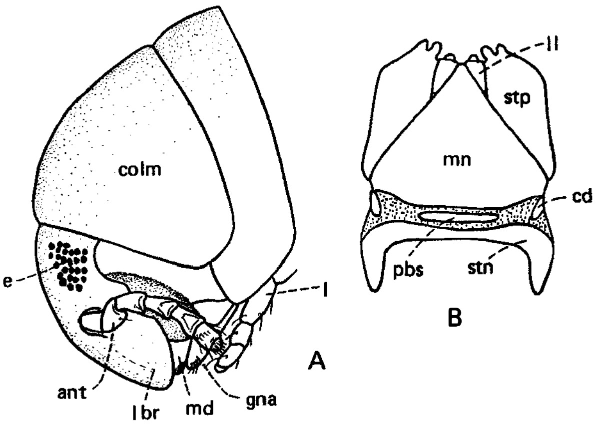

Figure 5–30 Head structure in a millipede (*Narceus*, order Spirobolida). A, Lateral view of head; B, Gnathochilarium. *ant*, antenna; *cd*, cardo; *colm*, collum, tergite of the first body segment; *e*, eye; *gna*, gnathochilarium; *l*, first leg; *lbr*, labrum; *ll*, lamina lingualis; *md*, mandible; *mn*, mentum; *pbs*, prebasilare; *stn*, sternum of first body segment; *stp*, stipes.

Millipedes are usually found in damp places: under leaves, in moss, under stones or boards, in rotting wood, or in the soil. Many species can give off an ill-smelling fluid through openings along the sides of the body. This fluid is sometimes strong enough to kill insects that are placed in a jar with the millipede, and it has been shown (in some cases at least) to contain hydrogen cyanide. Millipedes do not bite people. Most millipedes are scavengers and feed on decaying plant material, but some attack living plants and sometimes do serious damage in greenhouses and gardens, and a few are predaceous. These animals overwinter as adults in protected situations and lay their eggs during the summer. Some construct nestlike cavities in the soil in which they deposit their eggs; others lay their eggs in damp places without constructing any sort of nest. The eggs are usually white and hatch within a few weeks. Newly hatched millipedes have only three pairs of legs. The remaining legs are added in subsequent molts.

There are a number of arrangements of orders and families in this group. We follow the arrangement of Chamberlin and Hoffman (1958), which is outlined here (with alternate names or arrangements in parentheses):

Subclass Pselaphognatha (Pencillata)
    Order Polyxenida
Subclass Chilognatha
  Superorder Pentazonia (Opisthandria)
    Order Glomerida (Oniscomorpha)
  Superorder Helminthomorpha (Olognatha, Eugnatha)
    Order Polydesmida (Proterospermophora)
    Order Chordeumida (Chordeumatida, Nematophora)
    Order Julida (Opisthospermophora in part)
    Order Spirobolida (Opisthospermophora in part)
    Order Spirostreptida (Opisthospermophora in part)
    Order Cambalida (Opisthospermophora in part)
  Superorder Colobognatha
    Order Polyzoniida
    Order Platydesmida

Key to the Orders of Diplopoda

1.	Adults with 13 pairs of legs; integument soft; body hairs forming long lateral tufts; 2–4 mm in length	Polyxenida	p. 144
1′.	Adults with 28 or more pairs of legs; integument strongly sclerotized; body hairs not forming long tufts; larger millipedes	2	
2(1′).	Body with 14–16 segments and with 11–13 tergites; male gonopods at caudal end of body, modified from last 2 pairs of legs; southern and western United States	Glomerida	p. 144
2′.	Body with 18 or more segments; male gonopods modified from legs on seventh segment	3	
3(2′).	Head small, often concealed, the mandibles much reduced; 8 pairs of legs anterior to the male gonopods	4	
3′.	Head and mandibles of normal size; 7 pairs of legs anterior to the male gonopods	5	

4(3).	Tergites with median groove; gnathochilarium with most of the typical parts; usually pink in color	Platydesmida	p. 145
4′.	Tergites without median groove; gnathochilarium consisting of a single plate or several indistinctly defined plates; usually cream colored	Polyzoniida	p. 145
5(3′).	Body with 18–22 segments; eyes absent; body more or less flattened, with lateral carinae	Polydesmida	p. 144
5′.	Body usually with 26 or more segments; eyes usually present; body usually cylindrical or nearly so, and only rarely (some Chordeumida) with lateral carinae	6	
6(5′).	Terminal segment of body with 1–3 pairs of setae-bearing papillae; lateral carinae sometimes present; collum not overlapping head; sternites not fused with pleurotergites; body with 26–30 segments	Chordeumida	p. 145
6′.	Terminal segment without such papillae; lateral carinae absent; collum large, hoodlike, usually overlapping head; sternites usually fused with pleurotergites; usually 40 or more body segments	7	
7(6′).	Stipites of gnathochilarium broadly contiguous along midline behind laminae linguales	Julida	p. 145
7′.	Stipites of gnathochilarium not contiguous, but widely separated by mentum and laminae linguales (Figure 5–30B)	8	
8(7′).	Fifth segment with 2 pairs of legs; third segment open ventrally; fourth and following segments closed	9	
8′.	Fifth segment with 1 pair of legs; third segment closed ventrally	Spirobolida	p. 145
9(8).	Laminae linguales completely separated by mentum; both anterior and posterior pairs of gonopods present and functional, posterior pair usually with long flagella; no legs on segment 4	Cambalida	p. 145
9′.	Laminae linguales usually not separated by mentum; posterior pair of gonopods rudimentary or absent, anterior pair elaborate; 1 pair of legs each on segments 1–4	Spirostreptida	p. 145

***ORDER* Polyxenida:**[42] These millipedes are minute (2–4 mm in length) and soft-bodied, with the body very bristly. The group is a small one (five North American species), and its members are widely distributed but are not common. They are usually found under bark or in litter. The order contains a single genus, *Polyxenus*, in the family Polyxenidae.

***ORDER* Glomerida[43]—Pill Millipedes:** These millipedes are so called because they can roll themselves into a ball. They are short and wide and resemble isopods, but have more than seven pairs of legs. Males have the gonopods at the posterior end of the body and clasperlike. The appendages of the seventh segment are not modified. These millipedes occur in the southeastern states and in California. U.S. species are small (8 mm or less in length), but some tropical species, when rolled up, are nearly as big as golf balls.

***ORDER* Polydesmida:**[44] The polydesmids are rather flattened millipedes, with the body keeled laterally and the eyes much reduced or absent. The tergites are divided by a transverse suture, a little anterior to the middle of the segment, into an anterior prozonite and a posterior metazonite. The metazonite is extended laterally as a broad lobe. The first and last two body segments are legless; segments 2 to 4 each have a single pair of legs; and the remaining segments each bear two pairs of legs. The anterior pair of legs on the seventh segment of the male is modified into gonopods. The diplosomites (those segments bearing two pairs of legs) are continuously sclerotized rings. There are no sutures between tergites, pleurites, and sternites.

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[42] Polyxenida: *poly*, many; *xenida*, stranger or guest.

[43] Glomerida: from the Latin, meaning a ball of yarn (referring to the way these animals roll themselves into a ball).

[44] Polydesmida: *poly*, many; *desmida*, bands.

This is a large group, with about 250 North American species. Many are brightly colored, and most of them have scent glands. *Oxidus gracilis* (Koch), a dark brown to black millipede, 19–22 mm in length and 2.0–2.5 mm wide, is a common pest in greenhouses. This order is divided into 10 families, and its members occur throughout the United States.

ORDER **Chordeumida:**[45] These millipedes have 26–30 segments, and the terminal tergite bears one to three pairs of hair-tipped papillae (spinnerets). The body is usually cylindrical. The head is broad and free and not overlapped by the collum. One or both pairs of legs on the seventh segment of the male may be modified into gonopods. This relatively large group has about 170 species in North America. A few are predaceous.

Three suborders of Chordeumida occur in the United States. The suborder Chordeumidea, with nine families (some classifications place these millipedes in a single family, the Craspedosomatidae), are small (mostly 4–15 mm in length), soft-bodied millipedes with no keels on the metazonites and without scent glands; they are not very common. The suborder Lysiopetalidea, with one family, the Lysiopetalidae (= Callipodidae), contains larger millipedes, which are usually keeled. These millipedes can coil the body into a spiral. The secretions of the scent glands are milky white and very odoriferous. The suborder Striariidea, with one family (the Striariidae), have no scent glands, the anal segment three-lobed, and a high middorsal carina on the metazonite. These millipedes are mostly southern and western in distribution.

ORDER **Julida:**[46] This order and the next three are by some authorities combined into a single order, the Opisthospermophora. These four groups have a cylindrical body, with 40 or more segments. The collum is large and hoodlike and overlaps the head. Either both pairs of legs on the seventh segment of the male are modified into gonopods or one pair is absent. Scent glands are present. The diplosomites are not differentiated into prozonite and metazonite. The millipedes in the order Julida have the stipites of the gnathochilarium broadly contiguous along the midline behind the laminae linguales. Segment 3 and the terminal segment are legless; segments 1, 2, and 4 have one pair of legs each; and the remaining segments have two pairs of legs each. More than a hundred species of julids occur in North America, and some reach a length of about 90 mm.

ORDER **Spirobolida:**[47] The millipedes in this order differ from the Julida in having the stipites of the gnathochilarium separated (Figure 5–30B) and from the following two orders in having one pair of legs each on segments 1 to 5. This group contains about 35 North American species, including some of the largest. *Narceus americanus* (Beauvois), which is dark brown and narrowly ringed with red, may reach a length of 100 mm (Figure 5–29).

ORDER **Spirostreptida:**[48] The members of this order have one pair of legs each on segments 1–4, and the posterior pair of gonopods on the seventh segment of the male is rudimentary or absent. The stipites of the gnathochilarium are separated, but the laminae linguales are usually contiguous. This group is principally tropical, but three species occur in the Southwest.

ORDER **Cambalida:**[49] These millipedes are very similar to the Spirostreptida, but have the laminae linguales separated by the mentum, both pairs of legs on the seventh segment of the male modified into gonopods, and there are no legs on the fourth segment. The collum is quite large, and most species have prominent longitudinal ridges on the body. One species in this order, *Cambala annulata* (Say), is known to be predaceous.

SUPERORDER **Colobognatha.**[50] The members of this group have a small head and suctorial mouthparts, and the body is somewhat flattened, with 30 to 60 segments. The first pair of legs on the seventh segment of the male is not modified into gonopods. This superorder contains two orders, the Platydesmida[51] and Polyzoniida,[52] which may be separated by the characters given in the key. These orders are represented in the United States by one and two families, respectively. *Polyzonium bivirgatum* (Wood), which reaches a length of about 20 mm, occurs in rotten wood.

Class Chilopoda[53]—Centipedes

The centipedes are elongate, flattened animals with 15 or more pairs of legs (Figure 5–31). Each body segment bears a single pair of legs. The last two pairs are directed backward and often differ in form from the other pairs. The antennae consist of 14 or more segments. The genital openings are at the posterior end of the body, usually on the next to last segment. Eyes may be present or absent; if present, they usually consist of numerous ommatidia. The head bears a pair of mandibles and two pairs of maxillae. The second pair of max-

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[45] Chordeumida: from the Greek, meaning a sausage.

[46] Julida: from the Greek, meaning a centipede.

[47] Spirobolida: *spiro*, spiral; *bolida*, throw.

[48] Spirostreptida: *spiro*, spiral; *streptida*, twisted.

[49] Cambalida: derivation unknown.

[50] Colobognatha: *colobo*, shortened; *gnatha*, jaws.

[51] Platydesmida: *platy*, flat; *desmida*, bands.

[52] Polyzoniida: *poly*, many; *zoniida*, belt or girdle.

[53] Chilopoda: *chilo*, lip; *poda*, foot or appendage (referring to the fact that the poison jaws are modified legs).

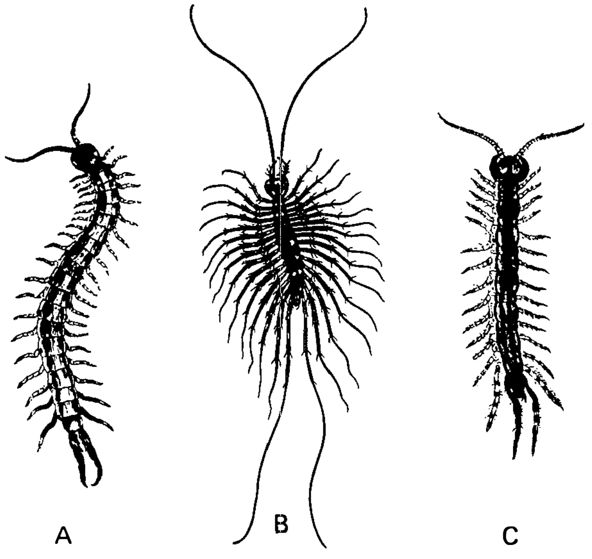

Figure 5–31 Centipedes. A, A large centipede, *Scolopendra obscura* Newport, about ¼ natural size; B, A house centipede, *Scutigera coleoptrata* (L.), about ½ natural size; C, A small centipede, *Lithobius erythrocephalus* Koch, about natural size. (Courtesy of USDA.)

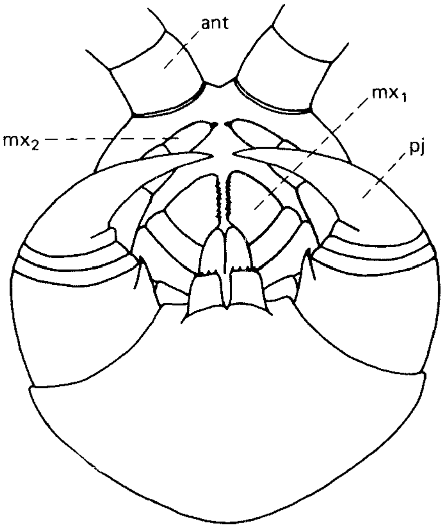

Figure 5–32 Head of centipede (*Scolopendra*, order Scolopendromorpha), ventral view. *ant*, antenna; mx_1, first maxilla; mx_2, second maxilla; *pj*, poison jaw or toxicognath, a modified leg.

illae may be somewhat leglike in form or short with basal segments of the two maxillae fused together. The appendages of the first body segment behind the head are clawlike and function as poison jaws (Figure 5–32).

Centipedes are found in a variety of places, but usually live in a protected situation such as in the soil, under bark, or in rotten logs. They are very active, fast-running animals and are predaceous. They feed on insects, spiders, and other small animals. All centipedes paralyze their prey with poison jaws. The smaller centipedes of the North are harmless to people, but the larger ones of the South and the tropics can inflict a painful bite. Centipedes overwinter as adults in protected situations and lay their eggs during summer. The eggs are usually sticky and become covered with soil, and are deposited singly. In some species the male may eat the egg before the female can cover it with soil.

Some centipedes produce silk, which is used in mating. The male makes a small web in which he deposits a package of sperm, and this package is then picked up by the female.

Key to the Orders of Chilopoda

1.	Adults with 15 pairs of legs, newly hatched young with 7 pairs (subclass Anamorpha)	2	
1′.	Adults and newly hatched young with 21 or more pairs of legs (subclass Epimorpha)	3	
2(1).	Spiracles unpaired, 7 in number, located on middorsal line near posterior margin of tergites; antennae long and many-segmented; legs long (Figure 5–31B); eyes compound	Scutigeromorpha	p. 147
2′.	Spiracles paired and located laterally; each leg-bearing segment with a separate tergite; antennae and legs relatively short (Figure 5–31C); eyes not compound, but consisting of single facets or groups of facets, or absent	Lithobiomorpha	p. 147

3(1′). Antennae with 17 or more segments; 21–23 pairs of legs; eyes usually 4 or more facets on each side — Scolopendromorpha p. 147

3′. Antennae 14-segmented; 29 or more pairs of legs; eyes absent — Geophilomorpha p. 147

***ORDER* Scutigeromorpha:**[54] This group includes the common house centipede, *Scutigera coleoptrata* (L.) (Figure 5–31B), which is found throughout the eastern United States and Canada. Its natural habitat is under logs and similar places, but it frequently enters houses, where it feeds on flies, spiders, and the like. In houses it often frequents the vicinity of sinks and drains. It is harmless to people. This order contains the single family Scutigeridae.

***ORDER* Lithobiomorpha[55]—Stone Centipedes:** These are short-legged, usually brown centipedes with 15 pairs of legs in the adults (Figure 5–31C). They vary in length from about 4 to 45 mm. Some members of this order are quite common, usually occurring under stones or logs, under bark, and in similar situations. When disturbed, they sometimes use their posterior legs to throw droplets of a sticky material at their attacker. This order contains two families, the Henicopidae (4–11 mm in length, the legs without strong spines, and the eyes consisting of a single facet each or absent) and the Lithobiidae (10–45 mm in length, at least some legs with strong spines, and the eyes usually consisting of many facets).

***ORDER* Scolopendromorpha:**[56] This group is principally tropical and, in the United States, occurs mainly in the southern states. The scolopendrids include the largest North American centipedes, which reach a length of about 150 mm (Figure 5–31A). Some tropical species may be a half a meter or more in length. Many scolopendrids are greenish or yellowish in color. These are the most venomous centipedes in our area; the bite of the larger species is quite painful, and they can also pinch with their last pair of legs. Two families occur in this order in the United States, the Scolopendridae (each eye with four facets) and the Cryptopidae (each eye with one facet).

***ORDER* Geophilomorpha[57]—Soil Centipedes:** The members of this order are slender, with 29 or more pairs of short legs and large poison jaws, and are usually whitish or yellowish. Most species are small, but some may reach a length of 100 mm or more. They usually live in soil, rotten logs, or in debris. When disturbed, they curl up and give off a secretion that seems to repel potential predators. The five families in this order in the United States are separated by characters of the mandibles.

Class Pauropoda[58]

Pauropods are minute, usually whitish myriapods, 1.0–1.5 mm in length. The antennae bear three apical branches. The nine pairs of legs are not grouped in double pairs as in the millipedes. The small head is sometimes covered by the tergal plate of the first body segment (Figure 5–33A). The genital ducts open near the anterior end of the body. Pauropods occur under stones, in leaf litter, and in similar places.

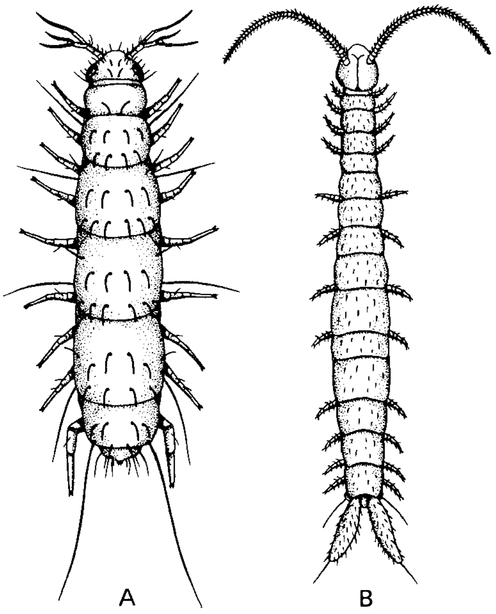

Figure 5–33 A, A pauropod, *Pauropus* sp., 95×; B, A symphylan, *Scolopendrella* sp., 16×. (A, Redrawn from Lubbock 1867; B, Redrawn from Comstock 1933, after Latzel.)

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[54] Scutigeromorpha: *scuti*, shield; *gero*, bear or carry; *morpha*, form.

[55] Lithobiomorpha: *litho*, stone; *bio*, life (*Lithobius* is a genus of centipede); *morpha*, form.

[56] Scolopendromorpha: *scolopendro*, centipede (*Scolopendra* is a genus of centipede); *morpha*, form.

[57] Geophilomorpha: *geo*, earth; *philo*, loving; *morpha*, form.

[58] Pauropoda: *pauro*, small; *poda*, foot or appendage.

Class Symphyla[59]

The symphylans are slender, whitish myriapods, 1–8 mm in length, with 15–22 (usually 15) body segments and 10–12 pairs of legs (Figure 5–33B). The antennae are slender and many-segmented, and the head is well developed and distinct. The genital openings are located near the anterior end of the body. Symphylans live in humus soil, under stones, in decaying wood, and in other damp situations. The garden symphylan, *Scutigerella immaculata* (Newport), feeds on the roots of plants and is sometimes a pest of vegetable crops, of the seedlings of broad-leaf trees, and in greenhouses.

Collecting and Preserving Myriapods

Myriapods may be killed in a cyanide bottle, but such specimens often become coiled or distorted. These animals are best killed and preserved in alcohol (about 75%) or in alcohol and glycerine (10 parts of alcohol to 1 part of glycerine). Millipedes may be picked up by hand or with forceps. Except in the case of the smaller specimens, it is well to handle centipedes with forceps, because the larger specimens can inflict a painful bite.

Class Hexapoda[60]

The class Hexapoda is included here to indicate its position in the phylum. Because the bulk of this book is concerned with this group, we say no more about them here.

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[59] Symphyla: from the Greek, meaning growing together.

[60] Hexapoda: *hexa*, six; *poda*, legs.

References

Aguinaldo, A. M. A., J. M. Turbeville, L. S. Linford, M. C. Rivera, J. R. Garey, R. A. Raff, and J. A. Lake. 1997. Evidence of a clade of nematodes, arthropods, and other moulting animals. Nature 387:489–493.

Anderson, D. T. 1973. Embryology and Phylogeny in Annelids and Arthropods. New York: Pergamon Press, 495 pp.

Barnes, R. D. 1987. Invertebrate zoology, 5th ed. Philadelphia: Saunders, 893 pp.

Brusca, R. C., and G. J. Brusca. 1990. Invertebrates. Sunderland, MA: Sinauer Associates, 922 pp.

Clarke, K. U. 1973. The Biology of Arthropods. New York: American Elsevier, 270 pp.

Cloudsley-Thompson, J. L. 1958. Spiders, Scorpions, Centipedes, and Mites. New York: Pergamon Press, 228 pp.

Eddy, S., and A. C. Hodson. 1950. Taxonomic Keys to the Common Animals of the North Central States Exclusive of the Parasitic Worms, Insects and Birds. Minneapolis: Burgess, 123 pp.

Edgecomb, G. D., G. D. F. Wilson, D. J. Colgan, M. R. Gray, and G. Cassis. 2000. Arthropod cladistics: combined analysis of histone H3 and U2 snRNAsequences and morphology. Cladistics 16:155–203.

Fortey, R. A., and R. H. Thomas (Eds.). 1997. Arthropod relationships. London: Chapman & Hall, 383 pp.

Fryer, G. 1997. A defence of arthropod polyphyly. In R. A. Fortey and R. H. Thomas (Eds.), Arthropod relationships, pp. 23–33. Chapman & Hall, London, 383 pp.

Giribet, G., and C. Ribera. 2000. A review of arthropod phylogeny: New data based on ribosomal DNA sequences and direct character optimization. Cladistics 16:204–231.

Gupta, A. P. 1979. Arthropod Phylogeny. New York: Van Nostrand Reinhold, 762 pp.

Levi, H. V., L. R. Levi, and H. S. Zim. 1968. Spiders and Their Kin. New York: Golden Press, 160 pp.

Manton, S. M. 1964. Mandibular mechanisms and the evolution of the arthropods. Phil. Trans. Roy. Soc. B 247:1–183.

Manton, S. M. 1977. The Arthropoda. Habits, Functional Morphology, and Evolution. Oxford, UK: Clarendon Press, 257 pp.

Pimentel, R. A. 1967. Invertebrate Identification Manual. New York: Reinhold, 150 pp.

Regier, J. C., and J. W. Shultz. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. Mol. Biol. Evol. 14:902–913.

Snodgrass, R. E. 1935. Principles of Insect Morphology. New York: McGraw-Hill, 677 pp.

Snodgrass, R. E. 1952. A Textbook of Arthropod Anatomy. Ithaca, NY: Comstock Associates, 363 pp.

Tiegs, O. W., and S. M. Manton. 1958. The evolution of the Arthropoda. Biol. Rev. 33:255–337.

Wägele, J.-W., and B. Misof. 2001. On quality of evidence in phylogeny reconstruction: a reply to Zrzavý's defence of the "Ecdysozoa" hypothesis. J. Zool. Syst. Evol. Res. 39:165–176.

Zrzavý, J. 2001. Ecdysozoa versus Articulata: clades, artifacts, prejudices. J. Zool. Syst. Evol. Res. 39:159–163.

Zrzavý, J., S. Mihulka, P. Kepka, A. Bezdìk, and D. Tietz. 1998. Phylogeny of the Metazoa based on morphological and 18S rDNA evidence. Cladistics 14:249–285.

The Chelicerata

Arthur, D. R. 1959. A Monograph of the Ixodoidea. Part V. The Genera *Dermacentor*, *Anocentor*, *Cosmiomma*, *Boophilus*, and *Margaropus*. Cambridge, UK: Cambridge University Press, 251 pp.

Baker, E. W., T. M. Evans, D. J. Gould, W. B. Hull, and H. L. Keegan. 1956. A Manual of Parasitic Mites of Medical or Economic Importance. New York: National Pest Control Association, 170 pp.

Baker, E. W., and G. W. Wharton. 1952. An Introduction to Acarology. New York: Macmillan, 465 pp.

Beatty, J. A. 1970. The spider genus *Ariadna* in the Americas (Araneae, Dysderidae). Bull. Mus. Comp. Zool., 139: 433–517.

Beck, L., and H. Schubart. 1968. Revision der Gattung *Cryptocellus* Westwood 1874 (Arachnida: Ricinulei). Senckenberg Biol. 49:67–78.

Bishop, S. C. 1949. The Phalangida (Opiliones) of New York, with special reference to the species in the Edmund Niles Huyk Preserve. Proc. Rochester Acad. Sci. 9(3):159–235.

Bristowe, W. S. 1958. The World of Spiders. London: Collins.

Carico, J. E. 1993. Revision of the genus *Trechalea* Thorell (Araneae, Trechaleidae) with a revision of the taxonomy of the Trechaleidae and Pisauridae of the Western Hemisphere. J. Arachnol. 21:226–257.

Chamberlin, J. C. 1931. The arachnid order Chelonethida. Stanford Univ. Publ. Biol. Ser. 7(1):1–284.

Coddington, J. A. 1986. The monophyletic origin of the orb web. In W. A. Shear (Ed.), Spiders: Webs, Behavior, and Evolution, pp. 319–363. Stanford, CA: Stanford University Press.

Coddington, J. A., and R. K. Colwell. 2001. Arachnids.In S. A. Levin (Ed.), Encyclopedia of Biodiversity, pp. 199–218. San Diego, CA: Academic Press.

Coddington, J. A., and H. W. Levi. 1991. Systematics and evolution of spiders (Araneae). Annu. Rev. Ecol. Syst. 22:565–592.

Corey, D. T., and D. J. Mott. A revision of the genus *Zora* (Araneae, Zoridae) in North America. J. Arachnol. 19:55–61.

Coyle, F. A. 1971. Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae, Antrodiaetidae). Bull. Mus. Comp. Zool. 141:269–402.

Coyle, F. A. 1981. The mygalomorph spider genus *Microhexura* (Araneae, Diplurdae). Bull. Amer. Mus. Nat. Hist. 170:64–75.

Coyle, F. A. 1988. A revision of the American funnel-web mygalomorph spider genus *Euagrus* (Araneae, Dipluridae). Bull. Amer. Mus. Nat. Hist. 187:203–292.

Dondale, C. D., and J. H. Redner. 1978. The crab spiders of Canada and Alaska (Araneae: Philodromidae and Thomisidae). The Insects and Arachnids of Canada. Part 5. Ottawa: Canadian Government Publishing Centre, 255 pp.

Dondale, C. D., and J. H. Redner. 1982. The sac spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae). The Insects and Arachnids of Canada. Part 9. Ottawa: Canadian Government Publishing Centre, 194 pp.

Dondale, C. D., and J. H. Redner. 1990. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). The Insects and Arachnids of Canada. Part 9. Ottawa: Canadian Government Publishing Centre, 383 pp.

Eberhard, W. G. 1977. Aggressive chemical mimicry by a bolas spider. Science 198:1173–1175.

Eberhard, W. G. 1980. The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneidae). Psyche 87:134–169.

Eberhard, W. G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. Evolution 36:1067–1095.

Eberhard, W. G. 1986. Web-building behavior of anapid, symphytognathid and mysmenid spiders (Araneae). J. Arachnol. 14:339–356.

Evans, G. O., J. H. Sheals, and D. Macfarlane. 1961. The Terrestrial Acari of the British Isles: An Introduction to Their Morphology, Biology, and Classification. London: British Museum, 219 pp.

Ewing, H. E. 1928. Scorpions of the western part of the United States, with notes on those occurring in northern Mexico. Proc. U.S. Natl. Mus. 73(9):1–24.

Ewing, H. E. 1929. A synopsis of the order Ricinulei. Ann. Entomol. Soc. Amer. 22:583–600.

Foelix, R. F. 1996. Biology of spiders, 2nd ed. New York: Oxford University Press.

Forster, R. R., and N. I. Platnick. 1977. A review of the spider family Symphytognathidae (Arachnida, Araneae). Amer. Mus. Nov. 2619:1–29.

Forster, R. R., and N. I. Platnick. 1985. A review of the austral spider family Orsolobidae (Arachnida, Aranaea), with notes on the superfamily Dysderoidea. Bull. Amer. Mus. Nat. Hist. 181:1–229.

Gertsch, W. J. 1958. The spider family Diguetidae. Amer. Mus. Nov. 1904:1–24.

Gertsch, W. J. 1958. The spider family Hypochilidae. Amer. Mus. Nov. 1912:1–28.

Gertsch, W. J. 1958. The spider family Plectreuridae. Amer. Mus. Nov. 1920:1–58.

Gertsch, W. J. 1973. The spider family Leptonetidae in North America. J. Arachnol. 1:145–203.

Gertsch, W. J. 1984. The spider family Nesticidae (Araneae) in North America, Central America, and the West Indies. Bull. Texas Mem. Mus. 31:1–91.

Gertsch, W. J., and F. Ennik. 1983. The spider genus *Loxosceles* in North America, Central America, and the West Indies (Araneae, Loxoscelidae). Bull. Amer. Mus. Nat. Hist. 175:264–360.

Gertsch, W. J., and S. Mulaik. 1939. Report on a new ricinuleid from Texas. Amer. Mus. Nov. No. 1037, 5 pp.

Gertsch, W. J., and N. I. Platnick. 1975. Revision of the trapdoor spider genus *Cyclocosmia* (Araneae, Cetnizidae). Amer. Mus. Nov. 2580:1–20.

Gertsch, W. J., and N. I. Platnick. 1979. A revision of the spider family Mecicobothriidae (Araneae, Mygalomorphae). Amer. Mus. Nov. 2687:1–32.

Gertsch, W. J., and N. I. Platnick. 1980. A revision of the American spiders of the family Atypidae (Araneae, Mygalomorphae). Amer. Mus. Nov. 2704:1–39.

Gosline, J. M., M. E. DeMont, and M. W. Denny. 1986. The structure and properties of spider silk. Endeavour 10:37–43.

Griswold, C. E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). Smithson. Contrib. Zool. 539:1–39.

Griswold, C. E., J. A. Coddington, N. I. Platnick, and R. R. Forster. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). J. Arachnol. 27:53–63.

Griswold, C. E., and D. Ubick. 2001. Zoropsidae: a spider family newly introduced to the USA (Araneae, Entelegynae, Lycosidae). J. Arachnol. 29:111–113.

Hodgkiss, H. E. 1930. The Eriophydae of New York: II. The maple mites. New York Agric. Expt. Sta., Geneva Tech. Bull. 163:5–45.

Hoff, C. C. 1949. The pseudoscorpions of Illinois. Ill. Nat. Hist. Surv. Bull. 24(4):411–498.

Hoff, C. C. 1959. List of the pseudoscorpions of North America north of Mexico. Amer. Mus. Nov. No. 1875, 50 pp.

Hormiga, G. 1994. A revision and cladistic analysis of the spider family Pimoidae. Smithson. Contrib Zool. 549:1–104.

Jocque, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bull. Amer. Mus. Nat. Hist., 201:1–160.

Johnson, J. D., and D. M. Allred. 1972. Scorpions of Utah. Gr. Basin Natur. 32(3):157–170.

Johnston, D. E. 1968. An Atlas of the Acari. I. The Families of Parasitiformes and Opilioacariformes. Columbus: Acarology Laboratory, Ohio State University, pp. 110.

Kaston, B. J. 1948. Spiders of Connecticut. Conn. State Geol. Nat. Hist. Surv. Bull. 70:1–874.

King, P. E. 1974. Pycnogonida. New York: St. Martin's, 144 pp.

Krantz, G. W. 1978. A Manual of Acarology, 2nd ed. Corvallis: Oregon State University Book Stores, 509 pp.

Leech, R. 1972. A revision of the Nearctic Amaurobiidae (Arachnida: Araneida). Mem. Ent. Soc. Can. 84:1–182

Lehtinen, P. T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Ann. Zool. Fenn. 4:199–468.

Maretić, Z. 1971. Latrodectism in Mediterranean countries, including South Russia, Israel, and North Africa. In Venomous Animals and Their Venoms. Vol. 3. Venomous Invertebrates. W. Bücherl, E. E. Buckley, V/ Deulofeu London: Academic Press.

Maretić, Z. 1975. European araneism. Bulletin of the Brit. Arachnol. Soc., 3:126–130.

Maretić, Z. 1983. Latrodectism: Variations in clinical manifestations provoked by *Latrodectus* species of spiders. Toxicon, 21:457–466.

Martens, J. 1978. Spinnenriere, Arachnida: Weberknechte, Opiliones. Die Tierwelt Deutschlands 64:1–464.

McCloskey, L. R. 1973. Marine flora and fauna of the northeastern United States: Pycnogonida. National Oceanic and Atmospheric Administration Tech. Rep. National Marine Fisheries Service, Seattle, WA, Circ. 386, 12 pp.

Muma, M. H. 1951–1962. The arachnid order Solpugida in the United States. Bull. Amer. Mus. Nat. Hist. 97:31–141. (1951). Amer. Mus. Nov. No. 2902, Suppl. 1, 44 pp. (1962).

Muma, M. H. 1953. A study of the spider family Selenopidae in North America, Central America, and the West Indies. Amer. Mus. Nov. 1619:1–55.

Muma, M. H. 1970. A synoptic review of North American, Central American, and West Indies Solpugida (Arthropoda: Arachnida). Arthropods of Florida and Neighboring Land Areas 5:1–62.

Opell, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bull. Mus. Comp. Zool. 148:443–549.

Opell, B. D. 1994. The ability of spider cribellar prey capture thread to hold insects with different surface features. Funct. Ecol. 8:145–150.

Osterhoudt, K. C., T Zaoutis, and J. J. Zorc. 2002. Lyme disease masquerading as brown recluse spider bite. Ann. Emerg. Med. 39:558–561.

Parrish, H. M. 1959. Deaths from bites and stings of venomous animals and insects. Amer. Med. Assoc. Arch. Intern. Med. 104:198–207.

Peakall, D. B. 1971. Conservation of web proteins in the spider *Araneus diadematus*. J. Exp. Zool. 176:257.

Peck, W. B. 1981. The Ctenidae of temperate zone North America. Bull. Amer. Mus. Nat. Hist. 170:157–169.

Peters, H. M. 1987. Fine structure and function of capture threads. In W. Nentwig (Ed.), Ecophysiology of Spiders, pp. 187–202. Berlin: Springer.

Platnick, N. I. 1990. Spinneret morphology and the phylogeny of ground spiders (Araneae, Gnaphosidae). Amer. Mus. Nov. 2978:1–42.

Platnick, N. I. 1994. A revision of the spider genus *Calponina* (Araneae, Caponiidae). Amer. Mus. Nov. 3100:1–15.

Platnick, N. I. 1995. A revision of the spider genus *Orthonops* (Araneae, Caponiidae). Amer. Mus. Nov. 3150:1–18.

Platnick, N. I. 1999. A revision of the Appalachian spider genus *Liocranoides* (Araneae: Tengellidae). Amer. Mus. Nov. 3285:1–13.

Platnick, N. I. 2003. The World Spider Catalog. Version 3.5. Available online atresearch.amnh.org/entomology/spiders/catalog81-87/index.html. 10 Nov., 2003.

Platnick, N. I., J. A. Coddington, R. R. Forster, and C. E. Griswold. 1991. Spinneret evidence and the higher classification of the haplogyne spiders (Araneae, Araneomorphae). Amer. Mus. Nov. 3016:1–73.

Platnick, N. I., and C. D. Dondale. 1992. The ground spiders of Canada and Alaska (Araneae: Gnaphosidae). The Insects and Arachnids of Canada. Part 19. Ottawa: Canadian Government Publishhing Centre, 297 pp.

Platnick, N. I., and R. R. Forster. 1990. On the spider family Anapidae (Araneae, Araneoidea) in the United States. J. New York Entomol. Soc. 98:108–112.

Platnick, N. I., and M. U. Shadab. 1978. A review of the spider genus *Mysmenopsis* (Araneae, Mysmenidae). Amer. Mus. Nov. 2661:1–22.

Platnick, N. I., and M. U. Shadab. 1989. A review of the spider genus *Teminius* (Araneae, Miturgidae). Amer. Mus. Nov. 3285:1–26.

Platnick, N. I., and D. Ubick. 1989. A revision of the spider genus *Drassinella* (Araneae, Liocranidae). Amer. Mus. Nov. 2937:1–24.

Platnick, N. I., and D. Ubick. 2001. A revision of the North American spiders of the New Genus *Socalchemmis* (Araneae, Liocranidae). Amer. Mus. Nov. 3339:1–25.

Pritchard, A. E., and E. W. Baker. 1955. A revision of the spider mite family Tetranychidae. Mem. Pac. Coast Entomol. Soc. 2:1–472.

Ramírez, M. J., and C. J. Grismado. 1997. A review of the spider family Filistatidae in Argentina (Arachnida, Araneae), with a cladistic reanalysis of filistatid genera. Entomol. Scand. 28:319–349.

Raven, R. J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bull. Amer. Mus. Nat. Hist. 182:1–180.

Reiskind, J. 1969. The spider subfamily Castianeirinae of North and Central America (Araneae, Clubionidae). Bull. Mus. Comp. Zool. 138:136–325.

Roth, V. 1984. The spider family Homalonychidae (Arachnida, Araneae). Amer. Mus. Nov. 2790:1–11.

Roth, V. 1993. Spider genera of North America, 3rd ed. Gainesville, FL:.American Arachnological Society.

Roth, V. D., and P. L Brame. 1972. Nearctic genera of the spider family Agelenidae (Arachnida, Araneida). Amer. Mus. Nov. 2505:1–52.

Sandlin, N. 2002. Convenient culprit. Amer. Med. News 45:37–38.

Savory,, T. 1977. Arachnida, 2nd ed. New York: Academic Press, 350 pp.

Schütt, K. 2000. The limits of the Araneoidea (Arachnida: Araneae). Aust. J. Zool. 48:135–153.

Shear, W. A. 1970. The spider family Oecobiidae in North America, Mexico, and the West Indies. Bull. Mus. Comp. Zool. 140:129–164.

Shear, W. A., J. M. Palmer, J. A. Coddington, and P. M. Bonamo. 1989. A Devonian spinneret: Early evidence of spiders and silk use. Science 246:479–481.

Stahnke, H. L. 1974. Revision and keys to the higher categories of Vejovidae (Scorpionida). J. Arachn. 1(2):107–141.

Thorp, R. W., and W. D. Woodson. 1976. The Black Widow Spider. New York: Dover.

Tuttle, D. M., and E. W. Baker. 1968. Spider Mites of Southwestern United States and Revisions of the Family Tetranychidae. Tuscon: University of Arizona Press, 150 pp.

Ubick, D., and N. I. Platnick. 1991. On *Hesperocranum*, a new spider genus from western North America (Araneae, Liocranidae). Amer. Mus. Nov. 3019:1–12.

Vetter, R. S., and D. K. Barger. 2002. An infestation of 2,055 brown recluse spiders (Araneae: Sicariidae) and no envenomations in a Kansas home: Implications for bite diagnoses in nonendemic areas. J. Med. Entomol. 39: 948–951.

Vetter, R. S., and S. P. Bush. 2002. Reports of presumptive brown recluse spider bites reinforce improbable diagnosis in regions of North America where the spider is not endemic. Clin. Infect. Dis. 35:442–445.

Vollrath, F. 1991. Leg regeneration in web spiders and its implications for orb weaver phylogeny. Bull. Brit. Arachnol. Soc. 8:177–184.

Vollrath, F. and D. P. Knight. 2001. Liquid crystalline spinning of spider silk. Nature 410:541–548.

Weygoldt, P. 1969. The Biology of Pseudoscorpions. Cambridge, MA: Harvard University Press, 145 pp.

The Crustacea

Crowder, W. 1931. Between the Tides. New York: Dodd, Mead, 461 pp.

Edmondson, W. T. (Ed.). 1959. Fresh Water Biology. New York: Wiley, 1248 pp.

Green, J. 1961. A Biology of the Crustacea. Chicago: Quadrangle Books, 180 pp.

Klots, E. B. 1966. The New Book of Freshwater Life. New York: Putnam's, 398 pp.

Kunkel, B. W. 1918. The Arthrostraca of Connecticut. Bull. Conn. Geol. Nat. Hist. Surv. 26:1–261.

Miner, R. W. 1950. Field Book of Seashore Life. New York: Putnam's, 888 pp.

Pennak, R. W. 1978. Fresh-Water Invertebrates of the United States, 2nd ed.. New York: Wiley Interscience, 803 pp.

Willoughby, L. G. 1976. Freshwater Biology. New York: Pica Press, 168 pp.

The Myriapods

Bailey, J. W. 1928. The Chilopoda of New York State, with Notes on the Diplopoda. N. Y. State Mus. Bull. 276:5–50.

Chamberlin, R. V., and R. L. Hoffman. 1958. Checklist of the millipedes of North America. U.S. Natl. Mus. Bull. 212:1–236.

Comstock, J. H. 1933. An introduction to entomology. Ithaca, NY: The Comstock Publishing Co., Inc., 1044 pp.

Eason, E. H. 1964. Centipedes of the British Isles. London: Frederick Wame, 294 pp.

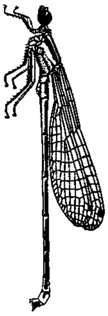
Johnson, B. M. 1954. The millipedes of Michigan. Pap. Mich. Acad. Sci. 39(1953):241–252.

Keeton, W. T. 1960. A taxonomic study of the millipede family Spirobolidae (Diplopoda, Spirobolida). Mem. Entomol. Soc. Amer. No. 17, 146 pp.

Shear, W. A. 1972. Studies in the millipede order Chordeumida (Diplopoda): A revision of the family Cleidogonidae and a reclassification of the order Chordeumida in the New World. Bull. Mus. Comp. Zool. Harvard 144(4):151–352.

6

Hexapoda[1]



Characters of the Hexapoda

The distinguishing characters of the Hexapoda may be listed briefly as follows (Wheeler et al. 2001): maxillary plate present (that is, with buccal cavity closed by second maxillae = labium); body divided into a distinct head, thorax, and abdomen; thorax with three pairs of legs; legs composed of six segments (coxa, trochanter, femur, tibia, tarsus, pretarsus); abdomen consisting of 11 segments; "knee" formed by the femoral–tibial joint; second maxillae fused to form the labium; epimorphic segmental growth; ommatidia with two primary pigment cells; trochantin present; arolium present. Many of these characters are attributed to the "ground plan" of Hexapoda, although researchers think a number of species later lost them. For quick identification, the hexapods can be recognized by the combination of the following:

1. Body with three distinct regions: head, thorax, and abdomen
2. One pair of antennae (rarely no antennae)
3. One pair of mandibles
4. One pair of maxillae
5. A hypopharynx
6. A labium
7. Three pairs of legs, one on each thoracic segment (a few insects are legless, and some larvae have additional leglike appendages—such as prolegs—on the abdominal segments)
8. The gonopore (rarely two gonopores) on the posterior portion of the abdomen
9. No locomotor appendages on the abdomen of the adult (except in some primitive hexapods); abdominal appendages, if present, located at the apex of the abdomen and consisting of a pair of cerci, an epiproct, and a pair of paraprocts

Classification of the Hexapoda

The class Hexapoda historically has been divided into orders primarily on the basis of the structure of the wings and mouthparts, and type of metamorphosis. Entomologists differ regarding the limits of some orders and their names. A few of the groups we treat as a single order some authorities divide into two or more, and some authorities combine into a single taxon two groups we recognize as separate orders. A few groups that we treat as orders of hexapods (the entognathous orders) some consider to be separate classes of arthropods. A synopsis of the orders of hexapods, as recognized in this book, is given in the following outline. Other names or arrangements are given in parentheses. Data on the sizes of the various orders are given in Table 6–1.

1. Protura (Myrientomata)—proturans
2. Collembola (Oligentomata)—springtails
3. Diplura (Entognatha, Entotrophi, Aptera)—diplurans

Insecta

4. Microcoryphia (Archaeognatha; Thysanura, Ectognatha, and Ectotrophi in part)—bristletails

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[1] Hexapoda: *hexa*, six; *poda*, foot.

Table 6–1 Relative Size of the Insect Orders

	Number of Species			
Order	North America[a]	Australia[b]	World Estimates[c]	Families in America North of Mexico[d]
Protura	73	30	500	3
Collembola	812	1,630	>6,000	12
Diplura	125	31	800	4
Microcoryphia	24	7	350	2
Thysanura	20	28	370	3
Ephemeroptera	599	84	2,000	21
Odonata	435	302	5,000	11
Orthoptera	1,210	2,827	>20,000	16
Phasmatodea	33	150	>2,500	4
Grylloblattodea	10	—	25	1
Mantophasmatodea	—	—	3	—
Dermaptera	23	63	1,800	6
Plecoptera	622	196	2,000	9
Embiidina	11	65	<200	3
Zoraptera	2	—	30	1
Isoptera	44	348	>2,300	4
Mantodea	30	162	1,800	2
Blattodea	67	428	<4,000	5
Hemiptera	11,298	5,650	35,000	90
Thysanoptera	695	422	4,500	7
Psocoptera	264	299	>3,000	28
Phthiraptera	941	255	>3,000	18
Coleoptera	24,085	28,200	>300,000	128
Neuroptera	400	649	5,500	15
Hymenoptera	20,372	14,781	115,000	74
Trichoptera	1,415	478	>7,000	26
Lepidoptera	11,673	20,816	150,000	84
Siphonaptera	314	88	2,380	8
Mecoptera	83	27	500	5
Strepsiptera	91	159	550	5
Diptera	19,782	7,786	>150,000	103
Total	95,553	78,175	826,108	698

[a] From R.W. Poole and P. Gentili (Eds.), 1996, *Nomina Insecta Nearctica*: A checklist of the insects of North America, 4 vols. (Rockville, MD: Entomological Information Services).

[b] From CSIRO (Ed.), 1991, The insects of Australia: A textbook for students and research workers, 2 vols (Carlton, Victoria, Australia: Melbourne University Press).

[c] Taken from numerous sources; the numbers are largely estimates based both on the number of described species and the number of species thought to remain undescribed and undiscovered.

[d] As used in this text.

5. Thysanura (Ectognatha, Ectotrophi, Zygentoma)—silverfish, firebrats

Pterygota—winged and secondarily wingless insects

6. Ephemeroptera (Ephemerida, Plectoptera)—mayflies
7. Odonata—dragonflies and damselflies
8. Orthoptera (Saltatoria, including Grylloptera)—grasshoppers and crickets
9. Phasmatodea (Phasmida, Phasmatida, Phasmatoptera, Cheleutoptera; Orthoptera in part)—walkingsticks and timemas
10. Grylloblattaria (Grylloblattodea, Notoptera)—rock crawlers
11. Mantophasmatodea
12. Dermaptera (Euplexoptera)—earwigs
13. Plecoptera—stoneflies

14. Embiidina (Embioptera)—webspinners
15. Zoraptera—zorapterans
16. Isoptera (Dictyoptera, Dictuoptera in part)—termites
17. Mantodea (Orthoptera, Dictyoptera, Dictuoptera in part)—mantids
18. Blattodea (Blattaria; Orthoptera, Dictyoptera, Dictuoptera in part)—cockroaches
19. Hemiptera (Heteroptera, Homoptera)—bugs, cicadas, hoppers, psyllids, whiteflies, aphids, and scale insects
20. Thysanoptera (Physapoda)—thrips
21. Psocoptera (Corrodentia)—psocids
22. Phthiraptera (Mallophaga, Anoplura, Siphunculata)—lice
23. Coleoptera—beetles
24. Neuroptera (including Megaloptera and Raphidiodea)—alderflies, dobsonflies, fishflies, snakeflies, lacewings, antlions, and owlflies
25. Hymenoptera—sawflies, ichneumonids, chalcidoids, ants, wasps, and bees
26. Trichoptera—caddisflies
27. Lepidoptera (including Zeugloptera)—butterflies and moths
28. Siphonaptera—fleas
29. Mecoptera (including Neomecoptera)—scorpionflies
30. Strepsiptera (Coleoptera in part)—twisted-wing parasites
31. Diptera—flies

Phylogeny of the Hexapoda

The hexapods are both a very old and a highly speciose group. Their evolutionary history and the development of hypotheses of their phylogeny have long been subjects of study. The data that form the basis of such work are the same for hexapods as for any other group: the comparative study of characters of both fossils (Table 6–2) and present-day species. The diversity, however, leads to a narrowing of the expertise of those

Table 6–2 An Outline of the Fossil Record

Era	Millions of Years Ago[a]	Periods		Forms of Life
Cenozoic	70	Pleistocene		First human
		Tertiary	Pliocene	Age of mammals and flowering plants; rise of modern insect genera; insects in amber
			Miocene	
			Oligocene	
			Eocene	
			Paleocene	
Mesozoic	135	Cretaceous		Age of reptiles; first flowering plants; most modern orders of insects; extinction of fossil insect orders
	180	Jurassic		First birds
	225	Triassic		First mammals
Paleozoic	270	Permian		Rise of most modern insect orders; extinction of many fossil orders
	350	Carboniferous		First winged insects (in several orders, most now extinct; some very large insects in this period); appearance of primitive reptiles
	400	Devonian		First hexapods (springtails); first land vertebrates (amphibians); age of fish
	440	Silurian		First land animals (scorpions and millipedes); rise of fish
	500	Ordovician		First vertebrates (ostracoderms)
	600	Cambrian		First arthropods (trilobites, xiphosurans, and branchiopods)
Precambrian				Primitive invertebrates

[a]From the beginning of the period.

who study hexapods and makes it difficult to recognize homologies across such a wide range of species. In recent years the widespread adoption of the principles of phylogenetic systematics, the emergence of molecular data as a new source of characters, the development of computer technologies and software, and the continued discovery of new taxa has led to a resurgence in interest in the study of phylogeny, particularly in the classical "problems" that have long interested systematists. The discussion that follows is based on the recent combined morphological and molecular analyses of Wheeler et al. (2001). This paper should be consulted for details of the synapomorphic characters for the higher taxa.

The fossil record for Precambrian time is quite scanty, but by the Cambrian period marine arthropods were present, consisting of trilobites, crustaceans, and xiphosurans. The first terrestrial arthropods—scorpions, spiders, and millipedes—appeared later, in the Silurian period, and the first hexapods appeared in the Devonian. Relatively few fossils are known from the Devonian, but many are known from the Carboniferous and later periods.

The hexapods are believed to have arisen from a myriapod-like ancestor that had paired leglike appendages on each body segment. The change to the hexapodous condition involved the development of a head, modification of the three segments behind the head as locomotory segments, and a loss or reduction of most of the appendages on the remaining body segments. The first hexapods were undoubtedly wingless and, therefore, are sometimes called *apterygotes.*

The Protura, Diplura, and Collembola are very distinct groups that were traditionally classified as insects. Many authorities now place them in three separate classes, some concluding that the characteristics of "hexapods" evolved at least four times independently (for example, see Manton 1977). Others reject that conclusion but agree with the classification, in so doing emphasizing the differences with the true insects. These three classes are primitively wingless and have the lateral portions of the head prolonged and fused to the labium to form a pouch, thus enveloping the mandibles and maxillae. This latter characteristic gives rise to the name of a taxon sometimes used to contain the three orders, the Entognatha. There is, as yet, no consensus on the pattern of relationships among these orders. The Protura and Collembola are often recognized as a monophyletic group, the Ellipura. The monophyly of the Diplura is disputed. These orders represent early offshoots of the hexapod line. The oldest known hexapod fossils (from the Devonian) are clearly identifiable as Collembola.

The other two primitively wingless orders are the Microcoryphia and Thysanura, also known as Archaeognatha and Zygentoma respectively. These creatures, as well as the winged insects, usually have exposed mouthparts (hence the name Ectognatha). Kristensen (1981) suggested restricting the word "*insects*" to refer to these ectognathous species and leaving *hexapods* to include both the entognathous orders and Ectognatha. Thus the terms "*insect*" and "*hexapod*" are not synonymous, and the more general word *hexapod* would refer to the fundamental characteristic of the species included, that is, having six thoracic legs. We use the terms in that sense in this book.

Two major lines developed within the winged insects, or Pterygota: the Paleoptera and the Neoptera; these two groups differ (among other ways) in their ability to flex their wings: the Paleoptera cannot flex their wings over the abdomen,[2] whereas the Neoptera can. This wing flexion is effected by rotating the third axillary sclerite about the posterior notal wing process (see Chapter 2). Several orders of Paleoptera were present in the late Paleozoic, but only the Ephemeroptera and Odonata have survived. The issue of whether the Paleoptera is a monophyletic group is still not definitively settled (see Wheeler et al. 2001; Hovmöller, Pape, and Källerjö 2002).

The relationships among the orders of Neoptera are far from clear. There are several orders, generally referred to as the *orthopteroid orders,* that generally are characterized by simple metamorphosis, mandibulate mouthparts, a large anal lobe in the hind wing, cerci, and numerous Malpighian tubules. They include the present orders Orthoptera, Phasmatodea, Grylloblattaria, Mantophasmatodea, Mantodea, Blattaria, Isoptera, Dermaptera, and Embiidina. Some authorities classify these together as the taxon Polyneoptera. Among these, the Grylloblattaria and Mantophasmatodea are wingless. The Embiidina do not have a large anal lobe in the hind wing, and it is uncertain whether this characteristic represents a secondary development. The position of the order Plecoptera is debated. They are sometimes placed within the Polyneoptera and sometimes separated by themselves in the group Paurometabola (or Pliconeoptera). Wheeler et al. (2001) partition these orders rather differently: they provide evidence for a monophyletic group composed of the Orthoptera, Phasmida, Grylloblattaria, and Dermaptera; another containing the Blattaria, Mantodea, Isoptera, and Zoraptera; and a third for the sister group relationship between Plecoptera and Embiidina. The Zoraptera are

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[2] An exception is the extinct order Diaphanapterodea. These insects could flex the wings by a mechanism different from that of the Neoptera (Kukalová-Peck 1991).

often classified with the Paraneoptera (see later) on the basis of the reduced number of Malpighian tubules and abdominal ganglia. The combined analysis groups this order with the so-called Dictyoptera (Mantodea, Blattaria, and Isoptera) on the basis of several morphological characters that are convergent in other orders, but also on the basis of a number of unambiguous molecular characters.

The hemipteroid groups (sometimes classified as the Paraneoptera)—Hemiptera, Thysanoptera, Psocoptera, and Phthiraptera—are characterized by simple metamorphosis, modification of the maxillary laciniae into stylets, absence of a large anal lobe in the hind wing and the venation somewhat reduced, no cerci, four Malpighian tubules, and biflagellate spermatozoa.

Complete metamorphosis appeared with the common ancestor of the remaining nine orders, the Holometabola or Endopterygota. The basal relationships among these orders are unsettled, but three major lines are usually recognized: (1) the Hymenoptera; (2) the neuropteroids: the Neuroptera and Coleoptera; and (3) the panorpoids: the Lepidoptera, Trichoptera, Mecoptera, Siphonaptera, Strepsiptera, and Diptera. The position of the Strepsiptera is a matter of some controversy. Typically they have been placed next to, or even within the Coleoptera. One of the most obvious characters supporting such a relationship is posteromotorism, that is, the use of only the hind wings for flying. Recent molecular analyses and follow-up morphological studies place the group as the sister to the true flies, Diptera (Whiting et al. 1997, Whiting 1998, Wheeler et al. 2001). Carmean and Crespi (1995) have argued that this is an artifact of phylogenetic analysis techniques, but the fact remains that the distribution of character states is now most simply reflected by hypothesizing that flies and Strepsiptera are each other's closest relatives.

These concepts of the phylogeny of the insect orders are summarized in the diagram in Figure 6–1, which also shows the sequence in which the orders are treated in this book.

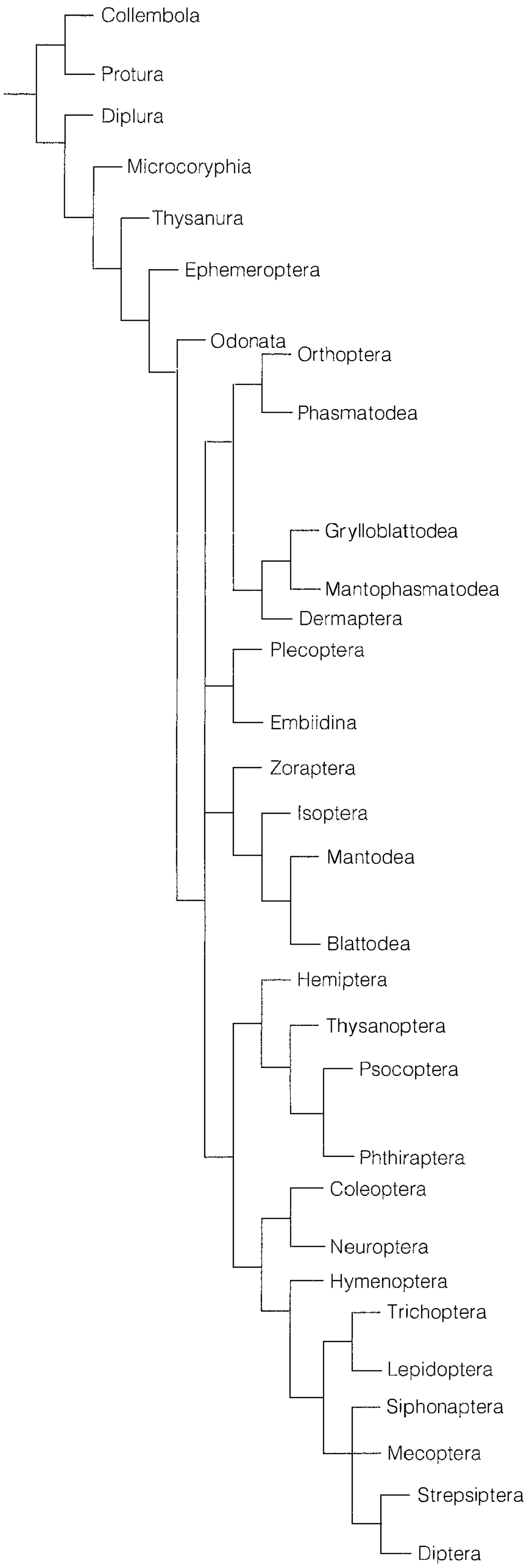

Figure 6–1 Phylogeny of the hexapod orders (after Wheeler et al. 2001).

Key to the Orders of Hexapods

This key includes adults, nymphs, and larvae. The portion of the key covering nymphs and larvae should work for most specimens, but some very young or highly specialized forms may not key out correctly. The habitat is sometimes an important character in keying out larvae. Groups marked with an asterisk (*) are unlikely to be encountered by the general collector.

1.	With well-developed wings (adults)	2	
1′.	Wingless or with wings vestigial or rudimentary (nymphs, larvae, and some adults)	28	
2(1).	Wings membranous, not hardened or leathery	3	
2′.	Front wings hardened or leathery, at least at base (Figure 6–2); hind wings, if present, usually membranous	23	
3(2).	With only 1 pair of wings	4	
3′.	With 2 pairs of wings	10	
4(3).	Body grasshopper-like; pronotum extending back over abdomen and pointed apically; hind legs enlarged (Figures 6–2A and 11–9) (pygmy grasshoppers, family Tetrigidae)	Orthoptera	p. 209
4′.	Body not grasshopper-like; pronotum not as in preceding item; hind legs not so enlarged	5	
5(4′).	Antennae with at least 1 segment bearing a long lateral process; front wings minute, hind wings fanlike (Figure 33–1A–D); minute insects (male twisted-wing parasites)	Strepsiptera*	p. 669
5′.	Not exactly fitting the preceding description	6	

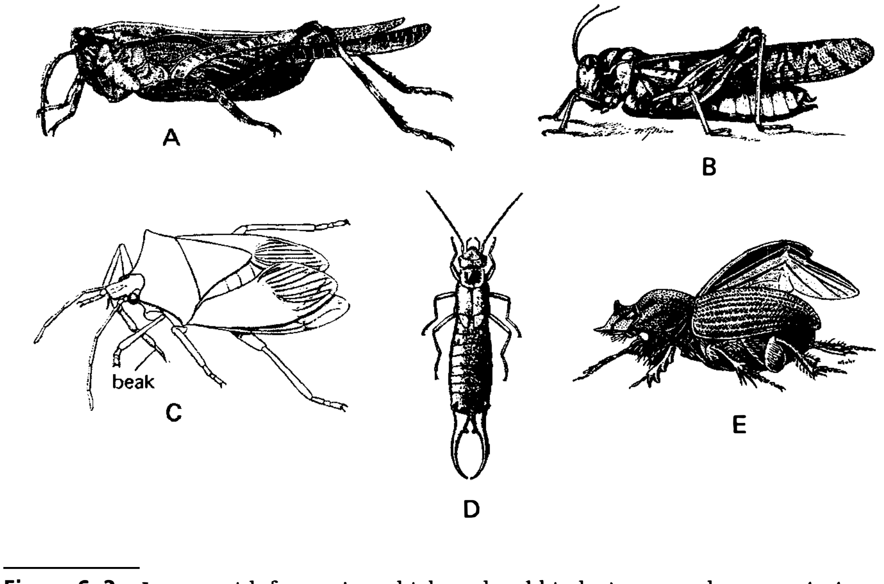

Figure 6–2 Insects with front wings thickened and hind wings membranous. A, A pygmy grasshopper (Orthoptera); B, A band-winged grasshopper (Orthoptera); C, A stink bug (Hemiptera); D, An earwig (Dermaptera); E, A dung beetle (Coleoptera). (A, C, and E courtesy of Illinois Natural History Survey; B, courtesy of USDA; D, courtesy of Knowlton and the Utah Agricultural Experiment Station.)

6(5′).	Abdomen with 1–3 threadlike or styletlike caudal filaments; mouthparts vestigial	7	
6′.	Abdomen without threadlike or styletlike caudal filaments; mouthparts nearly always well developed, mandibulate or haustellate (Figure 6–3)	8	
7(6).	Antennae long and conspicuous; abdomen terminating in long style (rarely 2 styles); wings with single forked vein (Figure 22–63A); halteres present, usually terminating in hooklike bristle; minute insects, usually less than 5 mm in length (male scale insects)	Hemiptera*	p. 268
7′.	Antennae short, bristlelike, inconspicuous; abdomen with two or three threadlike caudal filaments; wings with numerous veins and cells; halteres absent; usually over 5 mm in length (mayflies)	Ephemeroptera	p. 181
8(6′).	Tarsi nearly always 5-segmented; mouthparts haustellate; hind wings reduced to halteres (Figure 6–4A, hal) (flies)	Diptera	p. 672
8′.	Tarsi 2- or 3-segmented; mouthparts variable; hind wings reduced or absent, not haltere-like	9	
9(8′).	Mouthparts mandibulate (some psocids)	Psocoptera*	p. 341
9′.	Mouthparts haustellate (some planthoppers and a few leafhoppers)	Hemiptera	p. 268

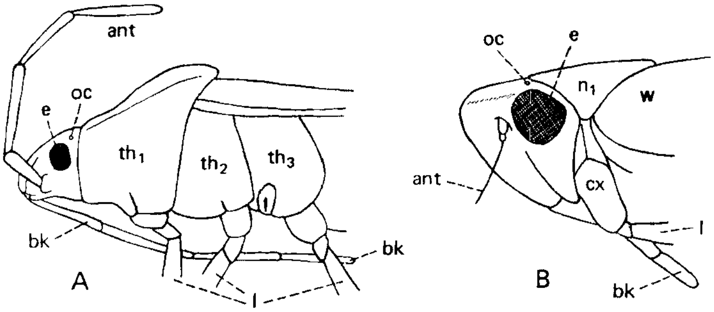

Figure 6–3 Lateral view of anterior part of body of A, A lygaeid bug (Hemiptera: Heteroptera) and B, A froghopper (Hemiptera: Auchenorrhyncha). *ant*, antenna; *bk*, beak; *cx*, front coxa; *e*, compound eye; *l*, legs; n_1, pronotum; *oc*, ocellus; th_{1-3}, thoracic segments; *w*, front wing.

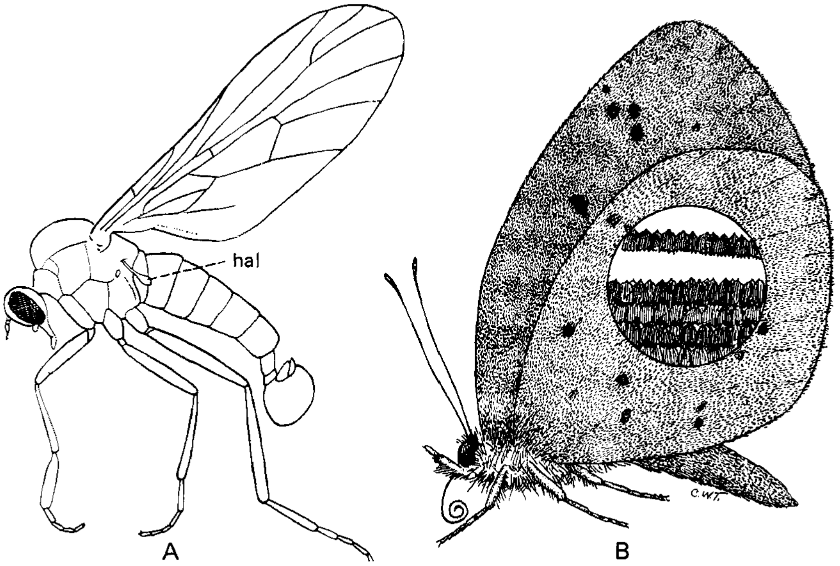

Figure 6–4 A, A dance fly (Diptera); B, A butterfly (Lepidoptera), with a section of the wing enlarged to show the scales. *hal*, haltere.

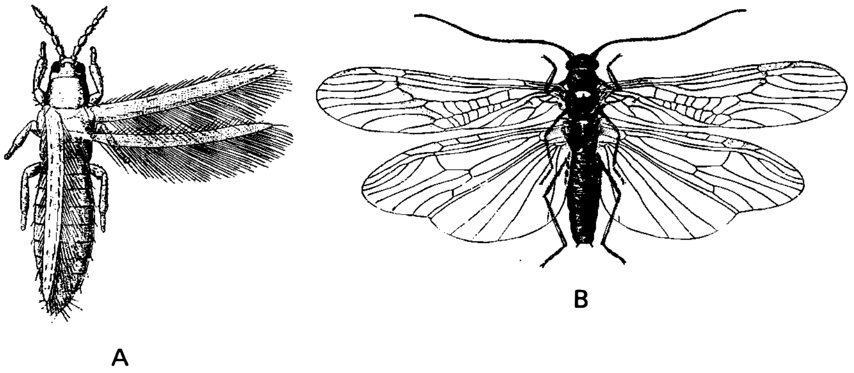

Figure 6–5 A, A thrips (Thysanoptera); B, A stonefly (Plecoptera). (A, Courtesy of Illinois Natural History Survey; B, Courtesy of USDA.)

10(3′).	Wings largely or entirely covered with scales; mouthparts usually in form of coiled proboscis; antennae many-segmented (Figure 6–4B) (butterflies and moths)	Lepidoptera	p. 571
10′.	Wings not covered with scales; mouthparts not in form of coiled proboscis; antennae variable	11	
11(10′).	Wings long and narrow, veinless or with only 1 or 2 veins, fringed with long hairs (Figure 6–5A); tarsi 1- or 2-segmented, last segment swollen; minute insects, usually less than 5 mm in length (thrips)	Thysanoptera	p. 333
11′.	Wings not as in preceding entry, or if wings are somewhat linear, then tarsi have more than 2 segments	12	
12(11′).	Front wings relatively large, usually triangular; hind wings small, usually rounded; wings at rest held together above body; wings usually with many veins and cells; antennae short, bristlelike, inconspicuous; abdomen with 2 or 3 threadlike caudal filaments (Figure 6–6); delicate, soft-bodied insects (mayflies)	Ephemeroptera	p. 181
12′.	Not exactly fitting the preceding description	13	
13(12′).	Tarsi 5-segmented	14	
13′.	Tarsi with 4 or fewer segments	17	
14(13).	Front wings noticeably hairy; mouthparts usually much reduced except for palps; antennae generally as long as body or longer; rather soft-bodied insects (caddisflies)	Trichoptera	p. 558
14′.	Front wings not hairy, at most with microscopic hairs; mandibles well developed; antennae shorter than body	15	
15(14′).	Rather hard-bodied, wasplike insects, abdomen often constricted at base; hind wings smaller than front wings, with fewer veins; front wings with 20 or fewer cells (sawflies, ichneumonids, chalcidoids, ants, wasps, and bees)	Hymenoptera	p. 481

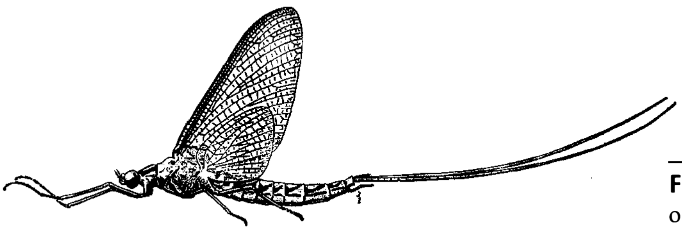

Figure 6–6 A mayfly (Ephemeroptera). (Courtesy of Illinois Natural History Survey.)

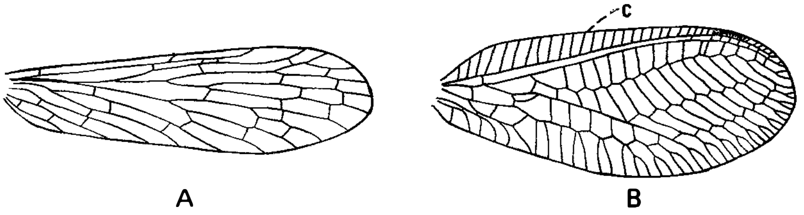

Figure 6–7 A, Front wing of a scorpionfly (Mecoptera); B, Front wing of a lacewing (Neuroptera).

15′.	Soft-bodied insects, not wasplike, abdomen not constricted at base; hind wings about same size as front wings and usually with about as many veins; front wings often with more than 20 cells	16	
16(15′).	Costal area of front wing nearly always with numerous crossveins (Figure 6–7B), or if not (Coniopterygidae, Figure 27-3A), then hind wings shorter than front wings; mouthparts not prolonged ventrally into beak (fishflies, dobsonflies, lacewings, and antlions)	Neuroptera	p. 469
16′.	Costal area of front wings with not more than 2 or 3 crossveins (Figure 6–7A); mouthparts prolonged ventrally to form beaklike structure (Figures 32–1A and 32–2) (scorpionflies)	Mecoptera	p. 662
17(13′).	Hind wings as long as front wings and of same shape or wider at base; wings at rest held above the body or outstretched (never held flat over abdomen); wings with many veins and cells; antennae short, bristlelike, inconspicuous; abdomen long, slender (Figure 6–8); tarsi 3-segmented; length 20–85 mm (dragonflies and damselflies)	Odonata	p. 193
17′.	Not exactly fitting the preceding description	18	
18(17′).	Mouthparts haustellate	Hemiptera	p. 268
18′.	Mouthparts mandibulate	19	
19(18′).	Tarsi 4-segmented; front and hind wings similar in size, shape, venation (Figure 19–1); cerci minute or absent (termites)	Isoptera	p. 252
19′.	Tarsi with 3 or fewer segments; hind wings usually shorter than front wings; cerci present or absent	20	
20(19′).	Hind wings with anal area nearly always enlarged and forming a lobe, which is folded fanwise at rest; venation varying from normal to very dense, the front wings usually with several crossveins between Cu_1 and M and between Cu_1 and Cu_2 (Figure 6–5B); cerci present, often fairly long; mostly 10 mm or more in length; nymphs aquatic, adults usually found near water (stoneflies)	Plecoptera	p. 239

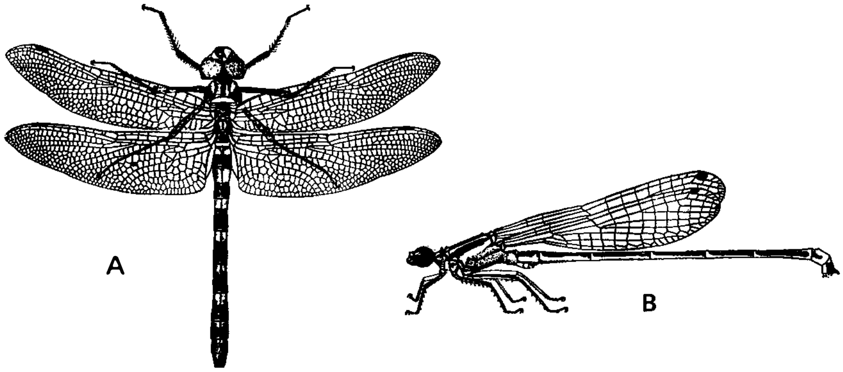

Figure 6–8 Odonata. A, A dragonfly; B, A damselfly. (Courtesy of Kennedy and the U.S. National Museum.)

20′.	Hind wings without enlarged anal area and not folded at rest, with no extra crossveins; cerci present (but short) or absent; mostly 10 mm in length or less; nymphs not aquatic, adults not necessarily near water	21	
21(20′).	Tarsi 3-segmented, basal segment of front tarsi enlarged (Figure 17–1) (webspinners)	**Embiidina***	p. 247
21′.	Tarsi 2- or 3-segmented, basal segment of front tarsi not enlarged	23	
22(21′).	Cerci present; tarsi 2-segmented; wing venation reduced (Figure 18–1A); antennae moniliform and 9-segmented	**Zoraptera***	p. 250
22′.	Cerci absent; tarsi 2- or 3-segmented; wing venation not particularly reduced (Figures 24–4 and 24–7); antennae not moniliform, usually long and hairlike, with 13 or more segments (Figure 24–8) (psocids)	**Psocoptera**	p. 341
23(2′).	Mouthparts haustellate, beak elongate and usually segmented (Figure 6–3)	**Hemiptera**	p. 268
23′.	Mouthparts mandibulate	24	
24(23′).	Abdomen with forcepslike cerci (Figure 6–2D); front wings short, leaving most of abdomen exposed; tarsi 3-segmented (earwigs)	**Dermaptera**	p. 234
24′.	Abdomen without forcepslike cerci, or if so, then front wings cover most of abdomen; tarsi variable	25	
25(24′).	Front wings without veins, usually meeting in straight line down middle of back; antennae generally with 11 or fewer segments; hind wings narrow, usually longer than front wings when unfolded, with few veins (Figure 6–2E) (beetles)	**Coleoptera**	p. 365
25′.	Front wings with veins, either held rooflike over abdomen or overlapping over abdomen when at rest; antennae generally with more than 12 segments; hind wings broad, usually shorter than front wings, with many veins (Figure 11-8), usually folded fanwise at rest	26	
26(25′).	Tarsi with 4 or fewer segments; usually jumping insects, with hind femora more or less enlarged (Figures 11–1, 11–6 through 11–10, 11-12, 11–14 through 11–18) (grasshoppers and crickets)	**Orthoptera**	p. 209
26′.	Tarsi 5-segmented; running or walking insects, with hind femora not particularly enlarged (Figures 20–1 and 21–3)	27	
27(26′).	Prothorax much longer than mesothorax; front legs modified for grasping prey (Figure 20–1) (mantids)	**Mantodea**	p. 260
27′.	Prothorax not greatly lengthened; front legs not modified for grasping prey (Figure 20–3) (cockroaches)	**Blattodea**	p. 263
28(1′).	Body usually insectlike, with segmented legs and usually also antennae (adults, nymphs, and some larvae)	29	
28′.	Body more or less wormlike, body regions (except possibly head) not well differentiated, segmented thoracic legs absent; antennae present or absent (larvae and some adults)	75	
29(28).	Front wings present but rudimentary; hind wings absent or represented by halteres; tarsi nearly always 5-segmented (some flies)	**Diptera***	p. 672
29′.	Wings entirely absent, or with 4 rudimentary wings and no halteres; tarsi variable	30	
30(29′).	Antennae absent; length 1.5 mm or less (Figure 7–1); usually occurring in soil or leaf litter (proturans)	**Protura***	p. 169
30′.	Antennae usually present (sometimes small); size and habitat variable	31	
31(30′).	Ectoparasites of birds, mammals, or honey bees and usually found on host; body more or less leathery, usually flattened dorsoventrally or laterally	32	

31′.	Free-living (not ectoparasitic), terrestrial or aquatic	35	
32(31).	Tarsi 5-segmented; antennae short, usually concealed in grooves on head; mouthparts haustellate	33	
32′.	Tarsi with fewer than 5 segments; antennae, mouthparts variable	34	
33(32).	Body flattened laterally; usually jumping insects, with relatively long legs (Figure 6–9A) (fleas)	Siphonaptera	p. 648
33′.	Body flattened dorsoventrally; not jumping insects, legs usually short (louse flies, bat flies, and bee lice)	Diptera*	p. 672
34(32′).	Antennae distinctly longer than head; tarsi 3-segmented (bed bugs and bat bugs)	Hemiptera	p. 268
34′.	Antennae not longer than head; tarsi 1-segmented (lice)	Phthiraptera	p. 356
35(31′).	Mouthparts haustellate, with conical or elongate beak enclosing stylets	36	
35′.	Mouthparts mandibulate (sometimes concealed in head), not beaklike	39	
36(35).	Tarsi 5-segmented; maxillary or labial palps present	37	
36′.	Tarsi with 4 or fewer segments; palps small or absent	38	
37(36).	Body covered with scales; beak usually in form of a coiled tube; antennae long and many-segmented (wingless moths)	Lepidoptera	p. 571
37′.	Body not covered with scales; beak not coiled; antennae variable, but often short, with 3 or fewer segments (wingless flies)	Diptera*	p. 672
38(36′).	Mouthparts in form of cone located basally on ventral side of head; palps present but short; body elongate, usually less than 5 mm in length; antennae about as long as head and prothorax combined, not bristlelike, 4- to 9-segmented; tarsi 1- or 2-segmented, often without claws (thrips)	Thysanoptera	p. 333
38′.	Mouthparts in form of an elongate segmented beak; palps absent; other characters variable	Hemiptera	p. 268
39(35′).	Abdomen distinctly constricted at base; antennae often elbowed; tarsi 5-segmented; hard-bodied, antlike insects (ants and wingless wasps)	Hymenoptera	p. 481

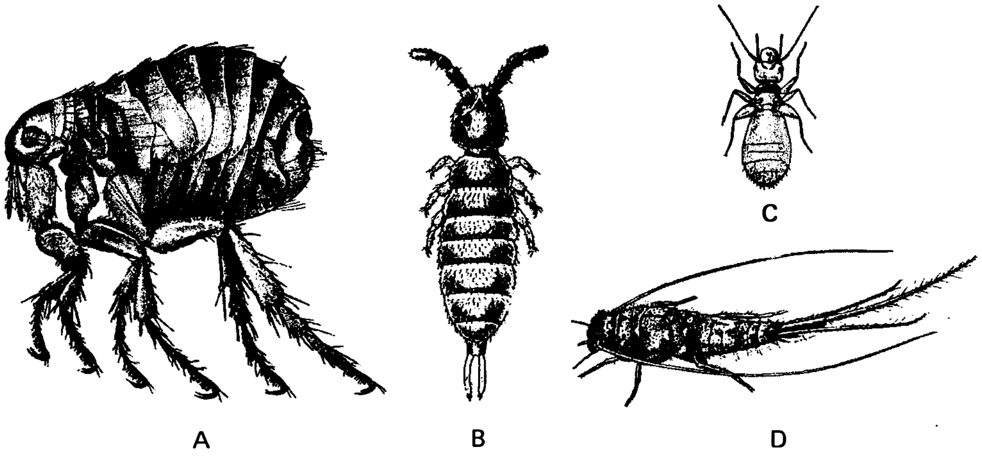

Figure 6–9 Wingless hexapods. A, Human flea (Siphonaptera); B, Springtail (Collembola); C, Psocid (Psocoptera); D, Firebrat (Thysanura). (A and C, Courtesy of USDA; B, Courtesy of Folsom and the U.S. National Museum; D, Courtesy of Illinois Natural History Survey.)

39′.	Abdomen not particularly constricted at base; antennae not elbowed; tarsi variable	40	
40(39′).	Abdomen with 3 long, threadlike caudal filaments and with stylelike appendages on some abdominal segments (Figure 6–9D); mouthparts mandibulate, but often more or less retracted into head; body nearly always covered with scales; terrestrial (silverfish, bristletails)	41	
40′.	Abdomen with only 2 threadlike caudal filaments or none; if with 3 (mayfly nymphs), then aquatic; other characters variable	42	
41(40).	Compound eyes large, usually contiguous; body somewhat cylindrical, with thorax arched; ocelli present; middle and hind coxae nearly always with styli; abdominal styli on segments 2–9 (Figure 8–1)	Microcoryphia	p. 177
41′.	Compound eyes small and widely separated, or absent; body somewhat flattened dorsoventrally, thorax not arched; ocelli present or absent; middle and hind coxae without styli; abdominal segments 1–6 usually without styli	Thysanura	p. 179
42(40′).	Aquatic, often with tracheal gills	43	
42′.	Terrestrial, without tracheal gills	50	
43(42).	Nymphs; compound eyes and usually wing pads present	44	
43′.	Larvae; compound eyes and wing pads absent	46	
44(43).	Labium prehensile, folded under head at rest, and when extended much longer than head (Figures 10–1G, 10–3, and 10–11B) (dragonfly and damselfly nymphs)	Odonata	p. 193
44′.	Labium normal, not as in preceding entry	45	
45(44′).	With 3 caudal filaments; tarsi with 1 claw; gills located on lateral margins of abdominal terga, usually leaflike or platelike (Figure 9–2) (mayfly nymphs)	Ephemeroptera	p. 181
45′.	With 2 caudal filaments; tarsi with 2 claws; gills (rarely absent) more or less fingerlike, usually located on underside of thorax (Figures 16–2B and 16–3) (stonefly nymphs)	Plecoptera	p. 239
46(43′).	With 5 pairs of prolegs on ventral side of abdominal segments, the prolegs with tiny hooks (crochets) (aquatic caterpillars)	Lepidoptera*	p. 571
46′.	Abdominal segments without prolegs or with terminal pair only	47	
47(46′).	Mouthparts consisting of 2 slender and elongate structures, longer than head; antennae long and slender, at least one third as long as body; tarsi with 1 claw (Figure 27–6D); living in freshwater sponges (larvae of Sisyridae)	Neuroptera	p. 469
47′.	Mouthparts, usually also antennae, short, not as in preceding entry	48	
48(47′).	Tarsi with 2 claws; abdomen with long slender lateral processes and a long slender terminal process (Sialidae, Figure 27–6C) or with slender lateral processes and a pair of hooklike structures apically (Corydalidae, Figure 27–6A,B) (fishfly and alderfly larvae)	Neuroptera	p. 469
48′.	Tarsi with 1 or 2 claws; if with 2, then abdomen not as in preceding entry	49	
49(48′).	Abdomen with pair of hooks, usually on anal prolegs, at posterior end and without long lateral processes (but sometimes with fingerlike gills); tarsi with 1 claw; usually living in cases (caddisfly larvae)	Trichoptera	p. 558
49′.	Abdomen with 4 hooks at posterior end (Figure 26–19A) or none, with or without long lateral processes (Figures 26–19 and 26–21); tarsi with 1 or 2 claws; not living in cases (beetle larvae)	Coleoptera	p. 365

50(42′).	Mouthparts usually withdrawn into head and not apparent; abdomen with stylelike appendages on some segments or with forked appendage near end of abdomen; usually less than 7 mm in length	51	
50′.	Mouthparts usually distinct, mandibulate or haustellate; abdomen without appendages such as described in preceding entry; size variable	52	
51(50).	Antennae long, many-segmented; abdomen with at least 9 segments, with stylelike appendages on ventral side of some segments; without forked appendage near end of abdomen, but with well-developed cerci (Figure 7–4) (diplurans)	Diplura*	p. 174
51′.	Antennae short, usually with 4 or fewer segments; abdomen with 6 or fewer segments, usually with forked appendage near posterior end (Figure 6–9B) (springtails)	Collembola	p. 170
52(50′).	Body larviform, thorax and abdomen not differentiated; compound eyes present (larviform female beetles)	Coleoptera*	p. 365
52′.	Body variable in shape, if larviform, then without compound eyes	53	
53(52′).	Compound eyes usually present; body shape variable, but usually not wormlike; wing pads often present (adults and nymphs)	54	
53′.	Compound eyes and wing pads absent; body usually wormlike in shape (larvae)	66	
54(53).	Tarsi 5-segmented	55	
54′.	Tarsi with 4 or fewer segments	60	
55(54).	Mouthparts prolonged ventrally into snoutlike structure (Figure 32–6); body more or less cylindrical, usually less than 15 mm in length (wingless scorpionflies)	Mecoptera*	p. 662
55′.	Mouthparts not as in preceding entry; body shape and size variable	56	
56(55′).	Antennae 5-segmented; Texas (some female twisted-wing parasites)	Strepsiptera*	p. 669
56′.	Antennae with more than 5 segments; widely distributed	57	
57(56′).	Cerci 1-segmented; body and legs very slender (Figure 12–1, 14–1)	58	
57′.	Cerci with 8 or more segments; body shape variable	59	
58(57).	Head prognathous; widely distributed	Phasmatodea	p. 227
58′.	Head hypognathous; known only from Africa	Mantophasmatodea*	p. 232
59(57′).	Body flattened and oval, head more or less concealed from above by pronotum (Figure 21–3); ocelli usually present; widely distributed (cockroaches)	Blattodea	p. 263
59′.	Body elongate and cylindrical, head not concealed from above by pronotum; ocelli absent; U.S. Northwest and western Canada (rock crawlers)	Grylloblattodea*	p. 230
60(54′).	Cerci forcepslike; tarsi 3-segmented	61	
60′.	Cerci absent or, if present, not forcepslike; tarsi variable	62	
61(60).	Antennae more than half as long as body; cerci short; western United States (timemas)	Phasmatodea*	p. 227
61′.	Antennae usually less than half as long as body; cerci long (Figure 6–2D); widely distributed (earwigs)	Dermaptera	p. 234
62(60′).	Tarsi 3-segmented, basal segment of front tarsi enlarged (Figure 17–1) (webspinners)	Embiidina*	p. 247
62′.	Tarsi 2- to 4-segmented, basal segment of front tarsi not enlarged	63	

63(62′).	Grasshopper-like insects, with hind legs enlarged and fitted for jumping; length usually over 15 mm (grasshoppers)	Orthoptera	p. 209
63′.	Not grasshopper-like, hind legs usually not as above; length less than 10 mm	64	
64(63′).	Tarsi 4-segmented; pale, soft-bodied, wood- or ground-inhabiting insects (termites)	Isoptera	p. 252
64′.	Tarsi 2- or 3-segmented; color and habits variable	65	
65(64′).	Cerci present, 1-segmented, terminating in long bristle; antennae 9-segmented, moniliform (Figure 18–1B–D); compound eyes and ocelli absent; tarsi 2-segmented (zorapterans)	Zoraptera*	p. 250
65′.	Cerci absent; antennae with 13 or more segments, usually hairlike (Figure 6–9C); compound eyes and 3 ocelli usually present; tarsi 2- or 3-segmented (psocids)	Psocoptera	p. 341
66(53′).	Ventral prolegs present on 2 or more abdominal segments (Figures 32–1B and 30–3)	67	
66′.	Abdominal prolegs absent or on terminal segment only	69	
67(66).	With 5 pairs of prolegs (on abdominal segments 3–6 and 10) or fewer, prolegs with tiny hooks (crochets); several (usually 6) stemmata on each side of head (caterpillars, butterfly and moth larvae)	Lepidoptera	p. 571
67′.	With 6 or more pairs of abdominal prolegs, prolegs without crochets; number of stemmata variable	68	
68(67′).	Seven or more stemmata on each side of head; prolegs on segments 1–8 or 3–8, usually inconspicuous, pointed structures (Figure 32–1B) (scorpionfly larvae)	Mecoptera*	p. 662
68′.	One stemma on each side of head; prolegs fleshy, not pointed, usually on abdominal segments 2–8 and 10, sometimes on 2–7 or 2–6 and 10 (Figure 28–37) (sawfly larvae)	Hymenoptera	p. 481
69(66′).	Mandible and maxilla on each side united to form sucking jaw that is often long (Figures 27–9B and 27–11); tarsi with 2 claws; labrum absent or fused with head capsule; maxillary palps absent (Planipennia: larvae of lacewings and antlions)	Neuroptera	p. 469
69′.	Mandibles and maxillae not as in preceding entry; tarsi with 1 or 2 claws; labrum and maxillary palps usually present	70	
70(69′).	Head and mouthparts directed forward (prognathous), head about as long along midventral line as along middorsal line, usually cylindrical or somewhat flattened	71	
70′.	Head and mouthparts directed ventrally (hypognathous), head much longer along middorsal line than along midventral line and usually rounded	73	
71(70).	Tarsi with 1 claw (some beetle larvae)	Coleoptera	p. 365
71′.	Tarsi with 2 claws	72	
72(71′).	Distinct labrum and clypeus present (Raphidioptera: snakefly larvae)	Neuroptera	p. 469
72′.	Labrum absent or fused with head capsule (most Adephaga: beetle larvae)	Coleoptera	p. 365
73(70′).	Front legs distinctly smaller than other pairs; middle and hind legs projecting laterally much more than front legs; small group of stemmata (usually 3) on each side of head behind bases of antennae; tarsal claws absent; length less than 5 mm; usually found in moss (larvae of Boreidae)	Mecoptera*	p. 662
73′.	Legs not as in preceding entry, front and middle legs about the same size and position; stemmata variable; tarsi with 1–3 claws; size and habitat variable	74	

74(73′).	Tarsi with 1 or 2 claws; abdomen usually without caudal filaments; antennae variable (beetle larvae)	Coleoptera	p. 365
74′.	Tarsi usually with 3 claws; abdomen with 2 caudal filaments about one third as long as body (Figure 33–1F); antennae usually short, 3-segmented (triungulin larvae of some beetles (Meloidae) and twisted-wing parasites)	Coleoptera* and Strepsiptera*	p. 365
75(28′).	Aquatic (fly larvae)	Diptera	p. 672
75′.	Not aquatic, but terrestrial or parasitic	76	
76(75′).	Sessile, plant feeding; body covered by a scale or waxy material; mouthparts haustellate, long and threadlike (female scale insects)	Hemiptera	p. 268
76′.	Not exactly fitting the preceding description	77	
77(76′).	Head and thorax more or less fused, abdominal segmentation indistinct (Figure 33–1G); internal parasites of other insects (female twisted-wing parasites)	Strepsiptera*	p. 669
77′.	Head not fused with thorax, body segmentation distinct; habitat variable	78	
78(77′).	Head distinct, sclerotized, usually pigmented and exserted	79	
78′.	Head indistinct, incompletely or not at all sclerotized, sometimes retracted into thorax	86	
79(78).	Head and mouthparts directed forward (prognathous), head about as long along midventral line as along middorsal line, usually cylindrical or somewhat flattened	80	
79′.	Head and mouthparts directed ventrally (hypognathous), head much longer along middorsal line than along midventral line and usually rounded	83	
80(79).	Terminal abdominal segment with a pair of short, pointed processes; several long setae on each body segment (flea larvae)	Siphonaptera*	p. 648
80′.	Not exactly fitting the description in the preceding entry	81	
81(80′).	Labium with protruding spinneret; antennae arising from membranous area at bases of mandibles; mandibles well developed, opposable; body usually more or less flattened; ventral prolegs usually with crochets; mostly leafminers in leaves, bark, or fruits (moth larvae)	Lepidoptera	p. 571
81′.	Labium without spinneret; antennae, if present, arising from head capsule; prolegs without crochets	82	
82(81′).	Mouthparts distinctly mandibulate, with opposable mandibles; spiracles usually present on thorax and 8 abdominal segments; body shape variable (beetle larvae)	Coleoptera	p. 365
82′.	Mouthparts as in preceding entry or with mouth hooks more or less parallel and moving vertically; spiracles variable, but usually not as in preceding entry; body elongate (fly larvae)	Diptera	p. 672
83(79′).	Abdominal segments usually with 1 or more longitudinal folds laterally or lateroventrally; body C-shaped, scarabaeiform (Figure 26–31); 1 pair of spiracles on thorax, usually 8 pairs on abdomen (white grubs: beetle larvae)	Coleoptera	p. 365
83′.	Abdominal segments without longitudinal folds, or if such folds present, then spiracles not as in preceding entry	84	
84(83′).	Head with adfrontal areas (Figure 30–3, adf); labium with projecting spinneret; antennae, if present, arising from membranous area at base of mandibles; often 1 or more (usually 6) stemmata on each side of head; ventral prolegs, if present, with crochets (moth larvae)	Lepidoptera	p. 571

84′.	Head without adfrontal areas; labium without spinneret; antennae and stemmata not as in preceding entry; prolegs, if present, without crochets	85	
85(84′).	Mandibles not heavily sclerotized and not brushlike; spiracles usually present on thorax and most abdominal segments, posterior pair not enlarged; larvae occurring in plant tissues, as parasites, or in cells constructed by adults (Apocrita)	Hymenoptera	p. 481
85′.	Mandibles usually brushlike; spiracles usually not as in preceding entry—if present in several abdominal segments, posterior pair much larger than others; occurring in wet places, in plant tissues, or as internal parasites (fly larvae, mostly Nematocera)	Diptera	p. 672
86(78′).	Mouthparts of normal mandibulate type, with opposable mandibles and maxillae; antennae usually present (beetle larvae)	Coleoptera	p. 365
86′.	Mouthparts reduced or modified, with only mandibles opposable, or with parallel mouth hooks present; antennae usually absent	87	
87(86′).	Body behind "head" (first body segment) consisting of 13 segments; full-grown larvae usually with sclerotized ventral plate ("breast bone") located ventrally behind head (larvae of Cecidomyiidae)	Diptera	p. 672
87′.	Body consisting of fewer segments; no "breast bone"	88	
88(87′).	Mouthparts consisting of 1 or 2 (if 2, then parallel, not opposable) median, dark-colored, decurved mouth hooks (maggots; larvae of Muscomorpha)	Diptera	p. 672
88′.	Mandibles opposable, but sometimes reduced, without mouth hooks as described in preceding entry (larvae of Apocrita)	Hymenoptera	p. 481

References

Arnett, R. H. 1985. American Insects: A Handbook of the Insects of America North of Mexico. New York: Van Nostrand Reinhold, 850 pp.

Borror, D. J., and R. E. White. 1970 (paperback ed., 1974). A Field Guide to the Insects of America North of Mexico. Boston: Houghton Mifflin, 404 pp.

Boudreaux, H. B. 1979. Arthropod Phylogeny with Special Reference to Insects. New York: Wiley, 320 pp.

Brues, C. T., A. L. Melander, and F. M. Carpenter. 1954. Classification of insects. Bull. Mus. Comp. Zool. Harvard No. 108, 917 pp.

Carmean, D., and B.J. Crespi. 1995. Do long branches attract flies? Nature 373:234.

Chinery, M. 1974. A Field Guide to the Insects of Britain and Northern Europe. Boston: Houghton Mifflin, 352 pp.

Chu, P. 1949. How to Know the Immature Insects. Dubuque, IA: William C Brown, 234 pp.

Commonwealth Scientific and Industrial Research Organization (CSIRO). 1970. The Insects of Australia. Carlton, Victoria: Melbourne University Press, 1029 pp.

Comstock, J. H. 1949. An Introduction to Entomology, 9th ed. Ithaca, NY: Comstock, 1064 pp.

Daly, H. V., J. T. Doyen, and P. R. Ehrlich. 1978. An Introduction to Insect Biology and Diversity. New York: McGraw-Hill, 564 pp.

Elzinga, R. J. 1981. Fundamentals of Entomology, 2nd ed. Englewood Cliffs, NJ: Prentice Hall, 432 pp.

Essig, E. O. 1958. Insects and Mites of Western North America. New York: Macmillan, 1050 pp.

Friedlander, C. P. 1977. The Biology of Insects. New York: Pica Press, 190 pp.

Grassé, P. P. (Ed.). 1949. Traité de Zoologie; Anatomie, Systématique, Biologie. Vol. 9. Insectes: Paleontologie, Géonémie, Aptérygotes, Ephéméroptères, Odonatoptères, Blattoptéroïdes, Orthoptéroïdes, Dermaptéroïdes, Coléoptères. Paris: Masson, 1117 pp.

Grassé, P. P. (Ed.). 1951. Traité de Zoologie: Anatomie, Systématique, Biologie, Vol. 10: Insectes Supérieurs et Hemiptéroïdes, Part I: Neuroptéroïdes, Mecoptéroïdes, Hemiptéroïdes, pp. 1–975, Part II: Hymenoptéroïdes, Psocoptéroïdes, Hemiptéroïdes, Thysanoptéroïdes, pp. 976–1948. Paris: Masson.

Hovmöller, R., T. Pape, and M. Källerjö. 2002. The Palaeoptera problem: Basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. Cladistics 18:313–323.

Imms, A. D. 1947. Insect Natural History. New York: Collins, 317 pp.

Jacques, H. E. 1947. How to Know the Insects, 2nd ed. Dubuque, IA: William C Brown, 205 pp.

Klass, K.-D., O. Zompro, N. P. Kristensen, and J. Adis. 2002. Mantophasmatodea: A new insect order with extant members in the Afrotropics. Science 296:1456–1459.

Kristensen, N. P. 1975. The phylogeny of hexapod "orders": A critical review of recent accounts. Z. Zool. Syst. Evolutions-Forsch. 13:1–44.

Kristensen, N. P. 1981. Phylogeny of insect orders. Annu. Rev. Entomol. 26:135–157.

Kukalová-Peck, J. 1991. Fossil history and the evolution of hexapod structures. In I. D. Naumann et al. (Eds.), The insects of Australia, 2nd ed., pp. 141–179. Melbourne: Melbourne University Press.

Linsenmaier, W. 1972. Insects of the World (translated from German by L. E. Chadwick). New York: McGraw-Hill, 392 pp.

Lutz, F. E. 1935. Field Book of Insects. New York: Putnam, 510 pp.

Manton, S.M. 1977. The Arthropoda. Habits, Functional Morphology, and Evolution. Oxford: Clarendon Press, 257 pp.

Martynov, A. V. 1925. Über zwei Grundtypen der Flügel bei den Insekten und ihre Evolution. Z. Morphol. Okol. Tiere 4:465–501.

Martynova, O. 1961. Paleoentomology. Annu. Rev. Entomol. 6:285–294.

Matheson, R. 1951. Entomology for Introductory Courses, 2nd ed. Ithaca, NY: Comstock, 629 pp.

Merritt, R. W., and K. W. Cummins. 1978. An Introduction to the Aquatic Insects of North America. Dubuque, IA: Kendall/Hunt, 512 pp.

Naumann, I. D., et al. (Eds.). 1991. Insects of Australia, 2nd ed. Melbourne: Melbourne University Press, 1137 pp.

Oldroyd, H. 1970. Elements of Entomology: An Introduction to the Study of Insects. London: Weidenfield & Nicolson, 312 pp.

Pennak, R. W. 1978. Fresh-Water Invertebrates of the United States, 2nd ed. New York: Wiley Interscience, 803 pp.

Peterson, A. 1939. Keys to the orders of immature insects (exclusive of eggs and pronymphs) of North American insects. Ann. Entomol. Soc. Amer. 32:267–278.

Peterson, A. 1948. Larvae of Insects. Part I. Lepidoptera and Plant-Infesting Hymenoptera. Ann Arbor, MI: Edwards, 315 pp.

Peterson, A. 1951. Larvae of Insects. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Ann Arbor, MI: Edwards, 416 pp.

Richard, O. W., and R. G. Davies. 1977. Imm's General Textbook of Entomology, vol. 1, pp. 1–418; vol. 2, pp. 419–1354. London: Chapman and Hall, 2 vols.

Romoser, W. S. 1973. The Science of Entomology. New York: Macmillan, 449 pp.

Ross, H. H. 1955. Evolution of the Insect Orders. Entomol. News 66:197–208.

Ross, H. H., C. A. Ross, and J. R. P. Ross. 1982, 4th ed. A Textbook of Entomology. New York: Wiley, 666 pp.

Smart, J. 1963. Explosive evolution and the phylogeny of the insects. Proc. Linn. Soc. Lond. 174:125–126.

Stehr, F. (Ed.). 1987. Immature Insects. Dubuque, IA: Kendall/Hunt, 754 pp.

Swain, R. B. 1948. The Insect Guide. New York: Doubleday, 261 pp.

Swan, L. A., and C. S. Papp. 1972. The Common Insects of North America. New York: Harper & Row, 750 pp.

Usinger, R. L. (Ed.). 1956. Aquatic Insects of California, with Keys to North American Genera and California Species. Berkeley: University of California Press, 508 pp.

Wheeler, W. C., M. Whiting, Q. D. Wheeler, and J. M. Carpenter. 2001. The phylogeny of the extant hexapod orders. Cladistics 17:113–169.

Whiting, M. F. 1998. Phylogenetic position of the Strepsiptera: Review of molecular and morphological evidence. Int. J. Insect Morphol. Embryol. 27:53–60.

Whiting, M. F., J. M. Carpenter, Q. D. Wheeler, and W. C. Wheeler. 1997. The Strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Syst. Biol. 46:1–68.

7

The Entognathous Hexapods: Protura, Collembola, and Diplura

These three orders and the two considered in Chapter 8 are all primitively wingless hexapods with simple metamorphosis; some of the pterygotes also lack wings, but their wingless condition is secondary, because they are derived from winged ancestors.

The three orders treated in this chapter are grouped together as the Entognatha because the mouthparts are more or less withdrawn into the head. The lateral portions of the head capsule are extended ventrally, fusing with the sides of the labium and labrum to form a pouch within which the mandibles and maxillae are concealed. In addition, in these orders the segments of the antennal flagellum (when present) are musculated, the tarsi are one-segmented; compound eyes are either absent or the ommatidia reduced in number (eight or less); and the tentorium is rudimentary.

Manton (1977) concluded that each of these three groups evolved the hexapodous condition independently and that each should be treated as a separate class. We follow here the conclusions of Boudreaux (1979) and the nomenclature suggestions of Kristensen (1981) and group them as the Entognatha. As such, they are the sister group of the insects (which includes the Microcoryphia, Thysanura, and Pterygota). Together the Entognatha and Insecta make up the Hexapoda.

There are other differences of opinion regarding the taxonomic status of these groups and the names to be given them. Our arrangement is outlined as follows, with synonyms and other arrangements in parentheses.

Order Protura (Myrientomata)—proturans
    Eosentomidae
    Protentomidae (including Hesperentomidae)
    Acerentomidae
Order Collembola—springtails
    Poduridae
    Hypogastruridae
    Onychiuridae
    Isotomidae
    Entomobryidae
    Neelidae
    Sminthuridae
    Mackenziellidae
    Tomoceridae
    Cyphoderidae
    Oncopoduridae
    Paronellidae
Order Diplura (Entotrophi)—diplurans
    Campodeidae
    Procampodeidae
    Anajapygidae
    Japygidae (Iapygidae)

Order Protura[1]—Proturans

The proturans are minute whitish hexapods, 0.6 to 1.5 mm in length. The head is somewhat conical, and there are no eyes or antennae (Figure 7–1). The mouthparts do not bite, but are apparently used to scrape off food particles that are then mixed with saliva and sucked into the mouth. The first pair of legs is principally sensory in function and is carried in an elevated position like antennae. The tarsi are one-segmented. Styli are present on the first three abdominal segments. On hatching

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[1] Protura: *prot*, first; *ura*, tail.

from the egg, the proturan abdomen consists of 9 segments. At each of the next three molts, segments are added anterior to the apical portion (the telson), so that the adult abdomen appears to have 12 segments (11 metameric segments and the apical telson).

These hexapods live in moist soil or humus, in leaf mold, under bark, and in decomposing logs. They feed on decomposing organic matter and fungal spores. They are found worldwide, and approximately 200 species are known at present.

Key to the Families of Protura

1.	Tracheae present, thorax with 2 pairs of spiracles; abdominal appendages 2-segmented, with a terminal vesicle	Eosemtomidae	p. 170
1′.	Tracheae and spiracles absent; abdominal appendages on segment 3, 1-segmented, appendages with or without terminal vesicle	2	
2(1′).	At least 2 pairs of abdominal appendages with terminal vesicle; most abdominal segments with single, transverse row of dorsal setae	Protentomidae	p. 170
2′.	Only first pair of abdominal appendages with terminal vesicle; most abdominal segments with 2 transverse rows of dorsal setae	Acerentomidae	p. 170

The Eosentomidae contain eight North American species, all belonging to the genus *Eosentomon*. The Protentomidae include three rather rare North American species, one recorded from Maryland, one from Iowa, and a third from California. The Acerentomidae are a widely distributed group, with eight North American species.

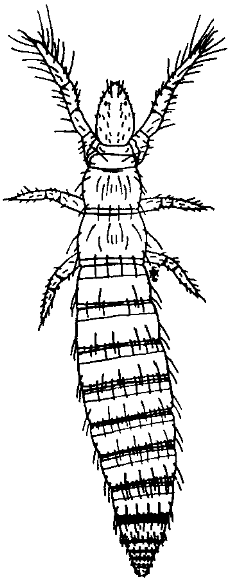

Figure 7–1 Dorsal view of a proturan, *Filientomon barberi barberi* (Ewing). (Courtesy of Ewing and the Entomological Society of America.)

Order Collembola[2,3]—Springtails

The common name "springtail" is derived from the forked structure or furcula that propels these minute hexapods through the air. Many Collembola (almost all Onychiuridae, many Hypogastruridae, and some Isotomidae) lack a furcula. The furcula arises on the ventral side of the fourth abdominal segment and, when at rest, is folded forward beneath the abdomen and held in place by a clasplike appendage on the third abdominal segment called the *retinaculum*. When disturbed the animal jumps by extending the furcula downward and backward. A springtail 3 to 6 mm in length may be able to leap 75 to 100 mm. A large number of species, especially those dwelling in soil, have reduced or totally atrophied spring mechanisms.

Many collembolans have up to eight ommatidia on each side of the head, whereas others have the ommatidia reduced or are totally blind. Mouthparts vary enormously, but generally are somewhat elongate and always concealed within the head. Although some species are carnivores or fluid feeders, most species feed on decaying vegetable material and fungi and have

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[2] Collembola: *coll*, glue; *embola*, a bolt or wedge (referring to the collophore).

[3] This section edited by Kenneth Christiansen.

mandibles with well developed molar plates. Others are fluid feeders and have styletlike mouthparts. The antennae are short, normally with four segments. The tarsi are one-segmented and fused with the tibiae. These hexapods have a tubelike appendage, the collophore, on the ventral side of the first abdominal segment; a bilobed, eversible vesicle may be protruded at its apex. Originally entomologists believed the collophore enabled the animal to cling to the surface on which it walked (hence the order name), but they now know this structure plays a role in water uptake and excretion.

Springtails, although very common and abundant, are seldom observed because of their small size (0.25 to 6 mm) and habit of living in concealed situations. Most species live in the soil or in such habitats as leaf litter, under bark, in decaying logs, and in fungi. Some species may be found on the surface of freshwater pools or along seashores; some occur on vegetation; and a few live in termite and ant nests, caves, or snow fields and glaciers. Springtail populations are often very large: up to $100,000/m^3$ of surface soil, or literally millions per hectare.

Most soil-inhabiting springtails feed on decaying plant material, fungi, and bacteria. Others feed on arthropod feces, pollen, algae, and other materials. A few species may occasionally cause damage in gardens, greenhouses, or mushroom cellars.

Key to the Families of Collembola

This key is adapted from Christiansen and Bellinger (1998).

1.	Abdominal segments 2–4 separated by dorsal sutures, or furcula rudimentary	2	
1′.	At least abdominal segments 2–4 fused dorsally; all furcal segments distinct	10	
2(1).	First thoracic segment distinct, visible dorsally, with dorsal setae	3	
2′.	First thoracic segment without dorsal setae and often not visible dorsally	5	
3(2).	Dens of furcula more than 3 times as long as manubrium, with distal rings of granules	Poduridae	p. 172
3′.	Dens absent or relatively short and not ringed	4	
4(3′).	Pseudocelli present at least on base of antenna or dorsum of abdominal segment 5	Onychiuridae	p. 172
4′.	Pseudocelli absent	Hypogastruridae	p. 172
5(2′).	Mucro of furcula hairy; antennal segment 4 shorter than 3; body with scales	Tomoceridae	p. 174
5′.	Mucro with 1–2 setae at most; antennal segment 4 at least as long as 3; body scales present or absent	6	
6(5′).	Dens with dentate spines; mucro length about equal to or greater than length of dens	Oncopoduridae	p. 174
6′.	Spines of dens simple (rarely) or absent; mucro usually much shorter than dens	7	
7(6′).	Postantennal organ (PAO) present or absent (in 3 species), usually smooth or unilaterally ciliate; scales absent	Isotomidae	p. 172
7′.	Postantennal organ (PAO) absent; some setae multilaterally ciliate; scales present	8	
8(7′).	Dens dorsally crenulate and curving upward in preserved specimens, basally in line with manubrium	Entomobryidae	p. 172
8′.	Dens not crenulate, straight	9	
9(8′).	Eyes and pigment absent; dens with large dorsal scales and without apical lobe	Cyphoderidae	p. 174
9′.	Eyes and pigment present; dens without dorsal scales, with apical lobe	Paronellidae	p. 174

10(1′).	Antennae shorter than head; eyes absent	Neelidae	p. 172
10′.	Antennae longer than head, or eyes with at least 1 facet, sometimes unpigmented	11	
11(10′).	Body elongate, oval; dens with 3 setae	Mackenziellidae	p. 174
11′.	Body globular; dens with many setae	Sminthuridae	p. 172

Family **Poduridae:** This family contains only one species, *Podura aquatica* L., a ubiquitous species that lives on the surface of freshwater ponds (Figure 7–2A). It is about 1.3 mm in length, and dark blue to reddish brown. This family is now considered to be more closely related to the Sminthuridae and Neelidae.

Family **Hypogastruridae:** Members of this family are usually 1–2 mm in length, with short appendages (sometimes with the furcula reduced or lacking), ranging from white, tan, purple, blue, and greenish, to black (Figure 7–2B). This is the largest family in the order, with 234 North American species. The snow flea, *Hypogastrura nivicola* (Fitch), is a dark-colored species often found grazing on algae and fungal spores on snow during the winter. It is sometimes a pest in buckets of maple sap. *Neanura muscorum* (Templeton) is a flat species with lobed body segments armed with short, strong setae, lacking a furcula, and lives beneath loose bark, rotting wood, or in leaf litter. It feeds on fungal juices and its mouthparts are formed into a cone. The seashore springtail, *Anurida maritima* (Guérin), is a slate-blue species that is sometimes extremely abundant along the northern Atlantic seashore between tidemarks, where it is found on the surface of small pools, under stones and shells, and crawling over the shore. These springtails cluster in air pockets under submerged rocks at high tide.

Family **Onychiuridae:** The members of this family (85 North American species) are somewhat similar to the Hypogastruridae. However, they differ markedly from that family by lacking pigment, eye patches, and a furcula (Figure 7–2C). They characteristically have pseudocelli (porelike structures) distributed on the antennal bases, head, and trunk segments. When disturbed, these creatures are capable of exuding noxious or toxic secretions through the pseudocelli. In culture, species of *Tullbergia* and *Onychiurus* have been shown to be parthenogenetic. This form of reproduction is probably common among these soil-dwelling species. Members of the Onychiuridae are abundantly found in agricultural and forest soils.

Family **Isotomidae:** The 197 North American members of this family range in color from white, yellow, and green to blue, brown, and dark purple with longitudinal stripes or transverse bands. Often occurring in vast numbers, *Isotomurus tricolor* (Packard), is a common species found in marshes, as well as wet forest edges, and sometimes freshwater pools (Figure 7–2D). *Metisotoma grandiceps* (Reuter) is carnivorous on other Collembola. *Isotoma propinqua* Axelson is one of several collembolan species that exhibit ecomorphosis, a phenomenon that occurs when individuals developed at abnormally high temperatures differ morphologically from those developing at lower temperatures, resulting in individuals that were earlier placed in different taxa.

Family **Entomobryidae:** This is a rather large group of species (138 North American species) of slender springtails that resemble the Isotomidae but have a large fourth abdominal segment (Figure 7–2E). In addition, some species have robust setae, scales, very long antennae and legs, and striking color combinations. *Orchesella hexfasciata* Harvey is a common yellow species with purple markings, and is found in leaf litter and under bark. *Lepidocyrtus paradoxus* Uzel is a dark blue species with a scaled body and enlarged mesothoracic segment, giving it the appearance of being "humpbacked." Another species, *Willowsia nigromaculata* (Lubbock) is found in close association with human structures and very protected habitats; it can be found in every old house. This is an extremely diverse family, which will probably be split into several families on future revision.

Family **Neelidae:** This is a small group (seven North American species) of very small springtails (0.27 to 0.70 mm in length) that have been collected in wooded areas and in caves. Most species are found in organic soils, caves, or under bark. They lack eyes, and the antennae are reduced in length to less than the diameter of the head (Figure 7–2G). Several members of the family are pigmented, but most are colorless. The thorax is relatively large, giving the animal a seedlike shape. *Megalothorax minimus* (Willem) is one of our commonest species, reaching a length of 0.4 mm.

Family **Sminthuridae:** These springtails (more than 100 North American species) range in size from 0.75 to 3 mm, and are oval-bodied active jumpers (Figure 7–2H). Many species are common on vegetation: some, such as

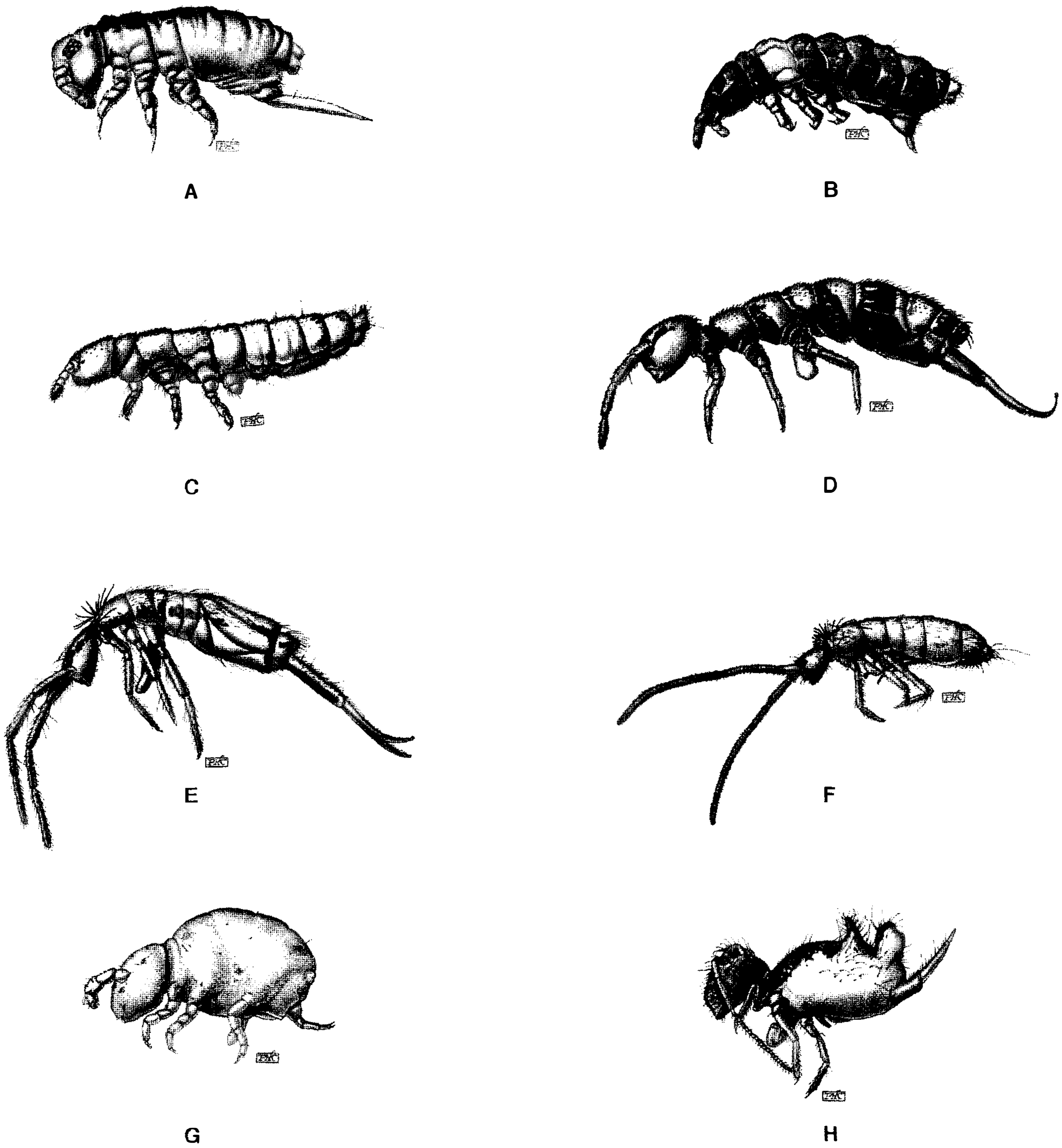

Figure 7–2 Springtails. A, *Podura aquatica* (L.) (Poduridae); B, *Pseudachorutes aureofasciatus* (Harvey) (Hypogastruridae); C, *Onychiurus ramosus* Folsom (Onychiuridae); D, *Isotomurus tricolor* (Packard) (Isotomidae); E, *Entomobrya socia* Denis (Entomobryidae); F, *Tomocerus elongatus* Maynard (Tomoceridae); G, *Neelus minutus* (Folsom) (Neelidae); H, *Sminthurus floridanus* MacGillivray (Sminthuridae). (Courtesy of Peter H. Carrington and R. J. Snider.)

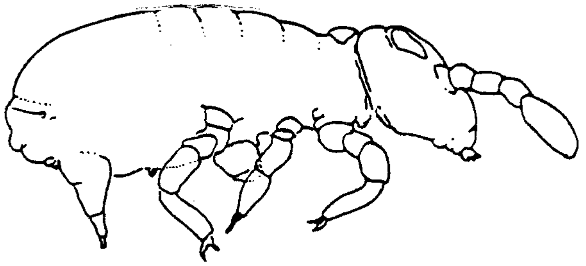

Figure 7–3 *Mackenziellia psocoides* Hammer, female (Mackenziellidae).

Bourletiella hortensis (Fitch), can be pests in gardens. Others, such as *Sminthurus viridis* L., can be devastating on alfalfa in New Zealand and Australia. Still others live under stones or bark or in leaf litter, and a few are found on freshwater pond surfaces. In woodland situations, *Ptenothrix atra* (L.) and *P. marmorata* (Packard) are often seen on mushrooms or living in old pine cones. Many species have elaborate mating habits.

Family **Mackenziellidae:** Members of this family have a linear, rather than a globular body (Figure 7–3), incomplete fusion of segments, and very simple, uniform setation. There is only a single known species, *Mackenziella psocoides* Hammer, described from northern Canada, but also known from Germany, Norway, and the Canary Islands.

Family **Tomoceridae:** Members of this family have coarsely ribbed scales and multilaterally ciliate setae. The fourth abdominal segment is shorter than or about equal to the length of the third (Figure 7–2F). There are 16 species in the Nearctic region, all in the genus *Tomocerus*, generally distributed in soil, litter, and caves. *Tomocerus flavescens* (Tullberg) and *T. elongatus* Maynard are commonly found in leaf litter and under bark. They are primarily nocturnal.

Family **Cyphoderidae:** Members of this family can be distinguished from entomobryids by the combined absence of ocelli, dental crenulations, and dental spines. They are facultative or obligatory commensals of social insects. Some tropical forms, including several known from Mexico, have highly modified legs or mouthparts for free existence. Only one species, *Cyphoderus similis* Folsom, occurs in the United States. It is widely distributed (California, Iowa, Massachusetts, New Jersey, and Louisiana), usually in association with ants.

Family **Oncopoduridae:** Members of this family have clear, hyaline scales and multilaterally ciliate setae. The furcula is densely scaled ventrally and has both simple and ciliate setae dorsally. The retinaculum is quadridentate, and all Nearctic species have a row of blunt setae dorsally on the fourth abdominal segment. There are two genera: *Harlomillisia*, with 1 species, *H. oculata* Mills (Florida, Georgia, North Carolina, Oregon, Tennessee, and Maryland); and *Oncopodura* with 11 species, found in litter, soil, and caves.

Family **Paronellidae:** In this family the fourth abdominal segment is greatly elongated. There are three widely distributed Nearctic species, all in the genus *Salina*.

Order Diplura[4]—Diplurans

The diplurans appear somewhat similar to the silverfish and bristletails, but they lack a median caudal filament and thus have only two caudal filaments or appendages. The body is usually not covered with scales; compound eyes and ocelli are absent; the tarsi are one-segmented; and the mouthparts are mandibulate and withdrawn into the head. The antennae are long and multisegmented; styli are present on abdominal segments 1–7 or 2–7. These hexapods are small (generally less than 7 mm in length) and usually pale in color. They are found in damp places in the soil, under bark, under stones or logs, in rotting wood, in caves, and in similar moist situations.

Key to the Families of Diplura

1.	Cerci (of adults) 1-segmented and forcepslike (Figure 7–4C)	2	
1′.	Cerci many-segmented, not forcepslike (Figure 7–4A,B)	3	
2(1).	Labial palpi lacking; antennal segment 4 without trichobothria	Parajapygidae	p. 175
2′.	Labial palpi present; antennal segments 4–6 with trichobothria	Japygidae	p. 175
3(1′).	Cerci long, about as long as antennae, and many-segmented (Figure 7–4A); widely distributed	Campodeidae	p. 175
3′.	Cerci short, shorter than antennae, and 8-segmented (Figure 7–4B); California	4	

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[4] Diplura: *dipl*, two; *ura*, tail.

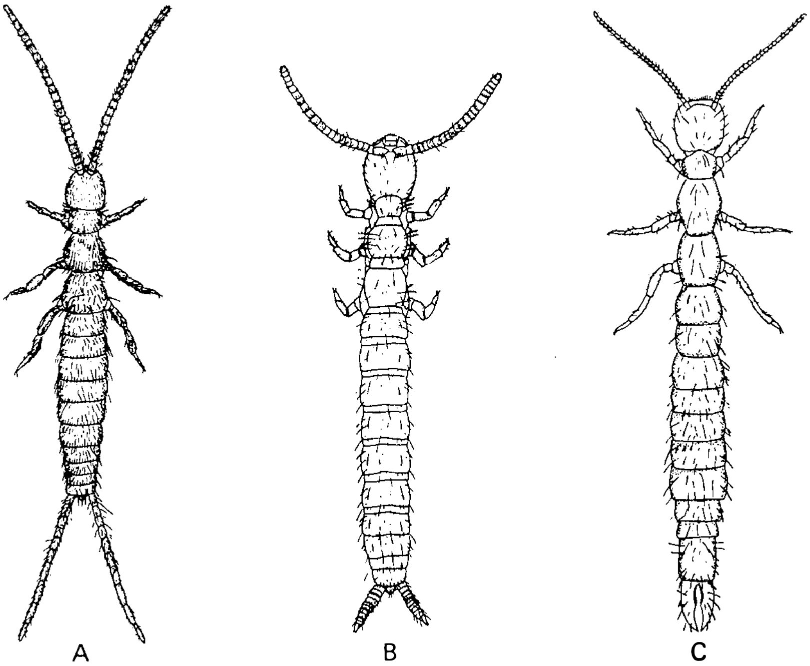


Figure 7–4 Diplurans. A, *Campodea folsomi* Silvestri (Campodeidae); B, *Anajapyx vesiculosus* Silvestri (Anajapygidae); C, *Holojapyx diversiungis* (Silvestri) (Japygidae).

4(3′).	Styli on abdominal segments 2–7; antennal trichobothria beginning on third segment	Procampodeidae	p. 175
4′.	Styli on abdominal segments 1–7; antennal trichobothria beginning on fifth segment	Anajapygidae	p. 175

Family **Campodeidae:** This is the largest family of diplurans (34 North American species), and contains those most often encountered. Most are about 6 mm long. *Campodea folsomi* Silvestri (Figure 7–4A) is a fairly common member of this family. It is found under stones in damp woods and in humus.

Family **Procampodeidae:** The only North American member of this family is *Procampodea macswaini* Condé and Pagés, which occurs in California.

Family **Anajapygidae:** This family is represented in the United States by a single rare species, *Anajapyx hermosa* Smith, which has been taken in wet soil and humus in Placer County, California.

Family **Japygidae:** This is a widely distributed group, but its members are not often encountered. Japygids and the next family can be recognized by the 1-segmented forcepslike cerci (Figure 7–4C). Twenty-eight species occur in the United States, and all are small. Some tropical species are larger, and one Australian species of *Heterojapyx* reaches a length of 50 mm.

Family **Parajapygidae:** A cosmopolitan group of some 40 species, with only two genera and 6 species found in the United States and Canada. Generally less than 15 mm in length, this family is distinguished from the Japygidae by the absence of trichobothria on the antennae.

Collecting and Preserving Entognatha

Most species can be collected by sifting debris or by looking under bark or stones or in fungi. Soil, leaf litter, or other material that may contain these species can be sprinkled onto a white surface and the animals found can be picked up with a moistened brush or aspirator. Many forms are most easily collected by means of a Berlese funnel (see Chapter 35). The springtails that occur on vegetation can be collected by sweeping the vegetation with a white enameled pan held at about a 30-degree angle to the ground. The hexapods falling or jumping into the pan can be easily seen and collected. The aquatic springtails can be collected with a dipper or tea strainer.

The best way to preserve these hexapods is in fluid—generally 80 to 85% alcohol. It is usually necessary to mount them on microscope slides for detailed study.

References

Bernard, E. C., and S. L. Tuxen. 1987. Class and order Protura. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 47–54. Dubuque, IA: Kendall/Hunt, 754 pp.

Betsch, J.-M. 1980. Eléments pour une monographie des Collemboles Symphyplèones (Hexapodes, Aptérygotes). Mem. Mus. Nat. Hist. Natur., Serie A 116:1–227.

Boudreaux, H. B. 1979. Arthropod phylogeny with special reference to insects. New York: Wiley, 320 pp.

Carapelli, A., F. Frati, F. Nardi, R. Dallai, and C. Simon. 2000. Molecular phylogeny of the apterygotan insects based on nuclear and mitochondrial genes. Pedobiologia 44:361–373.

Christiansen, K. 1964. Bionomics of Collembola. Annu. Rev. Entomol. 9:147–178.

Christiansen, K. A., and P. F. Bellinger. 1988. The Collembola of North America North of the Rio Grande. Grinnell, IA: Grinnell College, 1322 pp.

Christiansen, K. A., and R. J. Snider. 1984. Aquatic Collembola. In R. W. Merritt and K. W. Cummins (Eds.), An Introduction to the Aquatic Insects, 2nd ed., pp. 82–93. Dubuque, IA: Kendall/Hunt.

Ewing, H. E. 1940. The Protura of North America. Ann. Entomol. Soc. Amer. 33:495–551.

Fjellberg, A. 1985. Arctic Collembola I—Alaskan Collembola of the families Poduridae, Hypogastruridae, Odontellidae, Brachystomellidae, and Neanuridae. Entomol. Scand. Suppl. No. 21, 126 pp.

Gisin, J. 1960. Collembolenfauna Europas. Geneva: Muséum d'Histoire Naturelle, 312 pp.

Hopkin, S. 1997. The biology of springtails, Insecta: Collembola. New York: Oxford University Press, 300 pp.

Kristensen, N. P. 1981. Phylogeny of insect orders. Annu. Rev. Entomol. 26: 135–157.

Lubbock, J. 1873. Monograph of the Collembola and Thysanura. London: Royal Society of London, 276 pp.

Manton, S. M. 1977. The Arthropoda, Habits, Functional Morphology, and Evolution. Oxford, UK: Clarendon Press, 527 pp.

Paclt, J. 1956. Biologie der primär flugellosen insekten. Jena, Germany: Gustav Fischer, 258 pp.

Paclt, J. 1957. Diplura. Genera Insect. 212:1–122.

Richards, W. R. 1968. Generic classification, evolution, and biogeography of the Sminthuridae of the world (Collembola). Mem. Entomol. Soc. Can. 53:1–54.

Salmon, J. T. 1964–1965. An index to the Collembola. Bull. Roy. Soc. New Zealand No. 7. Vol. 1, pp. 1–144 (1964). Vol. 2, pp. 145–644 (1964). Vol. 3, pp. 645–651 (1965).

Smith, L. M. 1960. The families Projapygidae and Anajapygidae (Diplura) in North America. Ann. Entomol. Soc. Amer. 53:575–583.

Snider, R. J. 1987. Class and order Collembola. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 55–64. Dubuque, IA: Kendall/Hunt, 754 pp.

Szeptycki, A. 1979. Chaetotaxy of the Entomobryidae and Its Phylogenetical Significance: Morpho-Systematic Studies on Collembola. IV. Krakow: Polska Akademia Nauk, 218 pp.

Tuxen, S. L. 1959. The phylogenetic significance of entognathy in entognathous apterygotes. Smithson. Misc. Coll. 137:379–416.

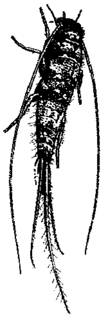
Tuxen, S. L. 1964. The Protura: A Revision of the Species of the World with Keys for Determination. Paris: Hermann, 360 pp.

Wygodzinsky, P. 1987. Class and order Diplura. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 65–67. Dubuque, IA: Kendall/Hunt, 754 pp.

8

The Apterygote Insects

Microcoryphia and Thysanura



The species in these two orders are small to medium-sized wingless creatures with simple metamorphosis. The Microcoryphia and Thysanura are the closest living relatives of the winged insects (see Figure 8–1), but they differ in a number of respects. Some features of thoracic structure in the Pterygota are correlated with the development of wings and are present even in the wingless members of that group. In the Pterygota each thoracic pleuron (with rare exceptions) is divided by a pleural suture into an episternum and epimeron, and the thoracic wall is strengthened internally by furcae and phragmata. The Microcoryphia and Thysanura have no pleural sutures, and furcae and phragmata are not developed. In addition, these orders usually have stylelike appendages on some of the pregenital abdominal segments. Adult Pterygota lack such appendages.

There are some differences between these orders and the other primitively wingless hexapods. The Microcoryphia and Thysanura are ectognathous; that is, the mouthparts are more or less exposed and not covered by cranial folds. The segments of the antennal flagellum are without muscles; the tarsi are three- to five-segmented; compound eyes are usually present; the tentorium is fairly well developed; and the abdomen has three long caudal filaments.

Microcoryphia[1]—Jumping Bristletails

The Microcoryphia resemble the silverfish in the order Thysanura. However, they are more cylindrical, with the thorax somewhat arched; the compound eyes are large and contiguous; ocelli are always present; each mandible has a single point of articulation with the head capsule[2]; the tarsi are three-segmented; and the middle and hind coxae usually bear styli. These styli are sometimes lacking on the middle coxae, or they may be completely absent. The abdomen bears a pair of styli on segments 2–9, and segments 2–7 each bear three ventral sclerites (the coxopodites and a median sternum; the sternum is sometimes much reduced). Segments 1–7 usually bear one or two pairs of eversible vesicles.

These insects live in grassy or wooded areas under leaves, under bark, in dead wood, under stones, under rocks and cliffs, and in similar situations. Most are nocturnal, and their eyes glow at night when illuminated with a flashlight. The largest members of the order are about 15 mm in length.

The Microcoryphia are quite active and jump when disturbed, sometimes as far as 25–30 cm. The eversible vesicles on the abdomen function as water-absorbing organs. Before these insects molt, they cement themselves to the substrate (the cement appears to be fecal material). If the cement fails, or if the substrate (such as sand) is not firm, they are unable to molt, and die. The bodies of these insects are covered with scales, which sometimes form distinctive patterns. The scales are often lost during the collecting process or when the insects are preserved in fluid. The jumping bristletails feed chiefly on algae, but feed also on lichens, mosses, decaying fruits, and similar materials.

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[1] Microcoryphia: *micro*, small; *coryphia*, head.

[2] The retention of this primitive form of mandibular articulation is reflected in the other name commonly used for this order, Archaeognatha: *archaeo*, old; *gnatha*, jaw.

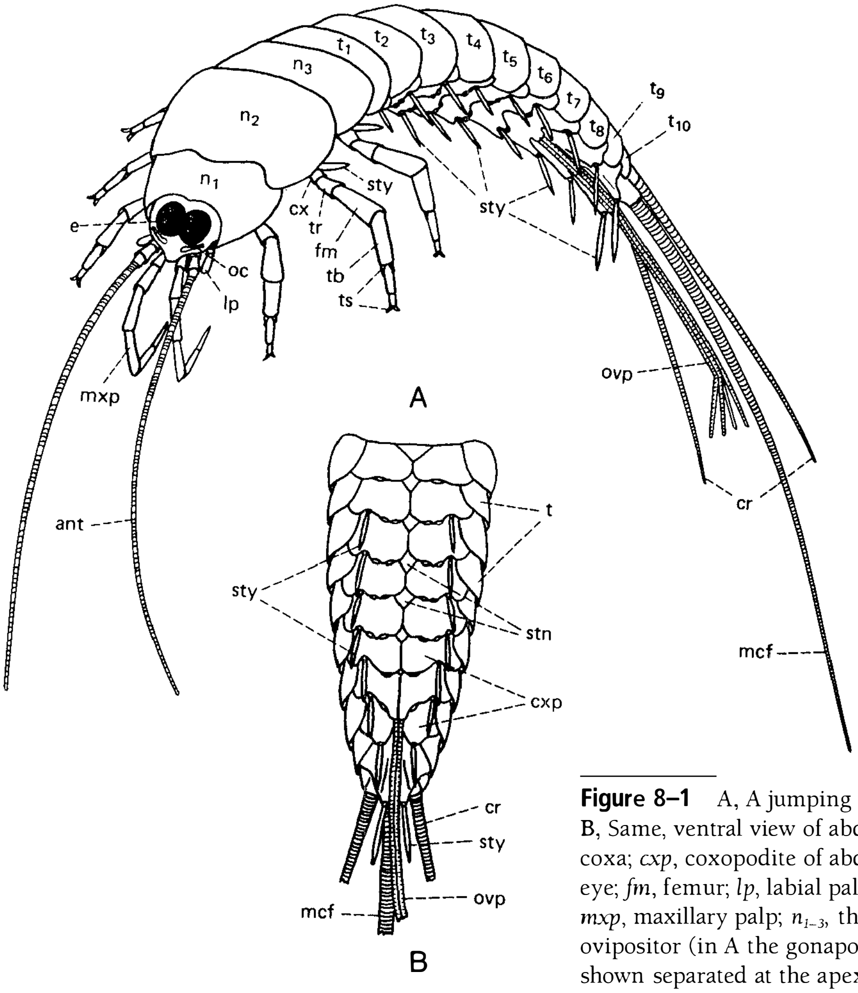

Figure 8–1 A, A jumping bristletail (Meinertellidae), female; B, Same, ventral view of abdomen. *ant*, antenna; *cr*, cerci; *cx*, coxa; *cxp*, coxopodite of abdominal appendages; *e*, compound eye; *fm*, femur; *lp*, labial palp; *mcf*, median caudal filament; *mxp*, maxillary palp; n_{1-3}, thoracic nota; *oc*, ocellus; *ovp*, ovipositor (in A the gonapophyses forming the ovipositor are shown separated at the apex); *stn*, abdominal sternites; *sty*, styli; *t*, terga; *tb*, tibia; *tr*, trochanter; *ts*, tarsus.

Key to the Families of Microcoryphia

1.	The 2 basal antennal segments heavily scaled; sterna of abdominal segments 2–7 large and triangular, extending caudad at least half the length of coxopodite; abdominal segments 2–7 with at least 1 pair of eversible vesicles, some segments with 2 pairs	Machilidae	p. 179
1′.	Antennae without scales; sterna of abdominal segments 2–7 very small, protruding only slightly or not at all between coxopodites, never extending as much as half the length of coxopodites (Figure 8–1B); abdominal segments 2–7 never with more than 1 pair of eversible vesicles, sometimes with none	Meinertellidae	p. 179

***Family* Machilidae:** These insects are brownish, elongate, and about 12 mm in length. There are 19 species in North America, and they are found in leaf litter, under bark, among rocks along the seashore, or in old stone walls. *Petrobius brevistylis* Carpenter is common in rocky cliffs along the New England seacoast, usually 5 to 20 feet above the high-tide mark.

***Family* Meinertellidae:** These are similar in appearance to the machilids and are widely distributed. Five species occur in North America.

Order Thysanura—Silverfish[3]

The silverfish are moderate-sized to small insects, usually elongated and somewhat flattened, with three tail-like appendages at the posterior end of the abdomen. The body is nearly always covered with scales. The mouthparts are mandibulate, and each mandible has two points of articulation with the head capsule. The compound eyes are small and widely separated (or absent), and ocelli may be present or absent. The tarsi are 3- to 5-segmented. The tail-like appendages consist of the cerci and a median caudal filament. The abdomen is 11-segmented, but the last segment is often much reduced. Segments 2–7 each contain a single undivided ventral sclerite or a sternite and a pair of coxopodites, and there are styli on segments 2–9, 7–9, or 8–9.

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[3] Thysanura: *thysan*, bristle or fringe; *ura*, tail.

Key to the Families of Thysanura

1.	Tarsi 5-segmented; ocelli present; body not covered with scales; northern California	Lepidotrichidae	p. 179
1′.	Tarsi 3- or 4-segmented; ocelli absent; body usually covered with scales	2	
2(1′).	Compound eyes present; body always covered with scales; widely distributed	Lepismatidae	p. 179
2′.	Compound eyes absent; body with scales (Atelurinae) or without scales (Nicoletiinae); Florida and Texas	Nicoletiidae	p. 179

***Family* Lepidotrichidae:** This family is represented in the United States by a single species, *Tricholepidion gertschi* Wygodzinsky, which lives under decaying bark of fallen Douglas fir in northern California. This insect is reddish, elongate, with a maximum body length of about 12 mm, with the antennae reaching a length of 9 mm and the caudal appendages 14 mm.

***Family* Nicoletiidae:** This group contains two subfamilies, which differ in appearance and habits. The Nicoletiinae are slender and 7–19 mm in length; they lack scales; and the caudal filaments and antennae are relatively long (half as long as the body or longer). The Atelurinae are oval (often with the body tapering posteriorly); the body is usually covered with scales; and the caudal filaments and antennae are shorter (usually less than half as long as the body). The Nicoletiinae are subterranean or occur in caves and mammal burrows. The Atelurinae are free-living or occur in ant or termite nests. Five species in this family have been reported from Florida and Texas.

***Family* Lepismatidae:** This group is represented in North America by 14 species, some of which are common and widely distributed. The best-known members of this family are the silverfish, *Lepisma saccharina* L., and the firebrat, *Thermobia domestica* (Packard), which are domestic species that live in buildings. They feed on all sorts of starchy substances and frequently become pests. In libraries they feed on starch in books, bindings, and labels. In dwellings they feed on starched clothing, curtains, linens, silks, and the starch paste in wallpaper. In stores they feed on paper, vegetables, and foods that contain starch. The silverfish is gray in color, about 12 mm in length, and is found in cool, damp situations. The firebrat (Figure 8–2) is tan or brown in color, about the same size as the silverfish, and frequents warm places around furnaces, boilers, and

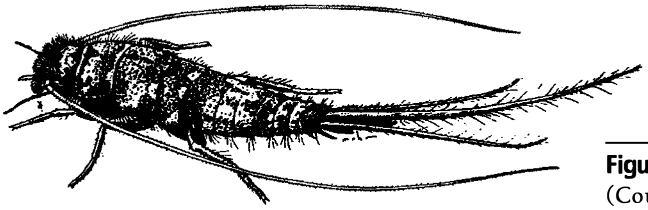

Figure 8–2 The firebrat, *Thermobia domestica* (Packard). (Courtesy of the Illinois Natural History Survey.)

steam pipes. Both species are quite active and can run rapidly. The lepismatids that occur outside buildings are found in caves, in debris, under stones and leaves, and in ant nests.

Collecting and Preserving Apterygote Insects

Indoor species such as the silverfish and firebrat can be trapped (see Chapter 35), or they can be collected with forceps or a moistened brush. Most outdoor species can be collected by sifting debris or by looking under bark or stones or in fungi. Soil, leaf litter, or other material that may contain these insects can be sprinkled onto a white surface, and the insects can be picked up with a moistened brush or aspirator. Many forms are most easily collected with a Berlese funnel. The jumping bristletails can sometimes be most easily collected at night by shining a flashlight over the rocks or leaf litter where they occur. In some 15–20 minutes the insects will begin crawling toward the light.

The best way to preserve these insects is in fluid—generally 80–85% alcohol. The bristletails are perhaps better preserved in alcoholic Bouin's solution.

References

Paclt, J. 1956. Biologie der primär flügellosen insekten. Jena, Germany: Gustav Fischer, 258 pp.

Paclt, J. 1963. Thysanura, family Nicoletiidae. Genera Insect., Fasc. 216e, 58 pp.; illus.

Remington, C. L. 1954. The suprageneric classification of the order Thysanura (Insecta). Ann. Entomol. Soc. Amer. 47:277–286.

Slabaugh, R. E. 1940. A new thysanuran, and a key to the domestic species of Lepismatidae (Thysanura) found in the United States. Entomol. News 51:95–98.

Smith, E. L. 1970. Biology and structure of some California bristletails and silverfish (Apterygota: Microcoryphia, Thysanura). Pan-Pac. Entomol. 46:212–225.

Wygodzinsky, P. 1961. On a surviving representative of the Lepidotrichidae (Thysanura). Ann. Entomol. Soc. Amer. 54:621–627.

Wygodzinsky, P. 1972. A revision of the silverfish (Lepismatidae, Thysanura) of the United States and the Caribbean area. Amer. Mus. Nov. No. 2481, 26 pp.

Wygodzinsky, P. 1987. Order Microcoryphia. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 68–70. Dubuque, IA: Kendall/Hunt, 754 pp.

Wygodzinsky, P. 1987. Order Thysanura. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 71–74. Dubuque, IA: Kendall/Hunt, 754 pp.

Wygodzinsky, P., and K. Schmidt. 1980. Survey of the Microcoryphia (Insecta) of the northeastern United States and adjacent provinces of Canada. Amer. Mus. Nov. No. 2071, 17 pp.

9

Order Ephemeroptera[1,2]
Mayflies

Mayflies are small to medium-sized, elongate, very soft-bodied insects with two or three long, threadlike tails. They are common near ponds and streams. The adults (Figure 9–1) have membranous wings with numerous veins. The front wings are usually large and triangular, and the hind wings are small and rounded. Some species have the front wings more elongate and the hind wings very small or absent. The wings at rest are held together above the body. The antennae are small, bristlelike, and inconspicuous. The immature stages are aquatic, and the metamorphosis is simple.

Mayfly nymphs are found in a variety of aquatic habitats. Some are streamlined in form and very active, and others are burrowing in habit. They can usually be recognized by the leaflike or plumose gills along the sides of the abdomen and the three (rarely two) long tails (Figure 9–2). Stonefly nymphs (Figures 16–2B and 16–3) are similar, but have only two tails (the cerci), and the gills are on the thorax (only rarely on the abdomen) and are not leaflike. Mayfly nymphs feed chiefly on algae and detritus. Many are most active at night.

When ready to transform to the winged stage, a mayfly nymph rises to the surface of the water and molts, and a winged form flies a short distance to the shore where it usually alights on vegetation. This stage, which is not the adult, is called a *subimago*. It molts once more, usually the next day, to become the adult. The subimago is dull in appearance and somewhat pubescent. There are hairs along the wing margin and on the caudal filaments (these areas are nearly always bare in the adults), and the genitalia are not fully developed. In a few genera there is no imago stage in the female; the subimago in these species mates and lays the eggs. The adult is usually smooth and shining; it has longer legs and tails than the subimago; and its genitalia are fully developed. The mayflies are the only insects that molt again after the wings become functional. The nymphs may require a year or two to develop, but the adults (which have vestigial mouthparts and do not feed) seldom live more than a day or two.

Adult mayflies often engage in rather spectacular swarming flights during which mating takes place. These swarms vary in size from small groups of individuals flying up and down in unison to large clouds of flying insects. The swarms of some species are 15 meters or more above the ground. The individuals in the swarm are usually all males. Sooner or later females enter the swarm, and a male will seize a female and fly away with her. Mating occurs in flight, and oviposition generally occurs very shortly thereafter (within minutes or, at most, a few hours).

The eggs are laid on the surface of the water or are attached to objects in the water. In cases where the eggs are laid on the surface of the water, they may simply be washed off the end of the abdomen a few at a time, or they may all be laid in one clump. Each species has characteristic egg-laying habits. A few species are ovoviviparous.

Mayflies often emerge in enormous numbers from lakes and rivers and sometimes may pile up along the shore or on nearby roads and streets. Piles as deep as 1.2 meters have been observed in Illinois (Burks 1953), causing serious traffic problems. Such enormous emergences are often a considerable nuisance. Up until about the mid-1950s, mass emergences of this sort oc-

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[1] Ephemeroptera: *ephemera*, for a day, short-lived; *ptera*, wings (referring to the short life of the adults).

[2] This chapter edited by Manuel L. Pescador.

Figure 9–1 A mayfly, *Hexagenia bilineata* (Say) (Ephemeridae). (Courtesy of Needham and the Bureau of Fisheries.)

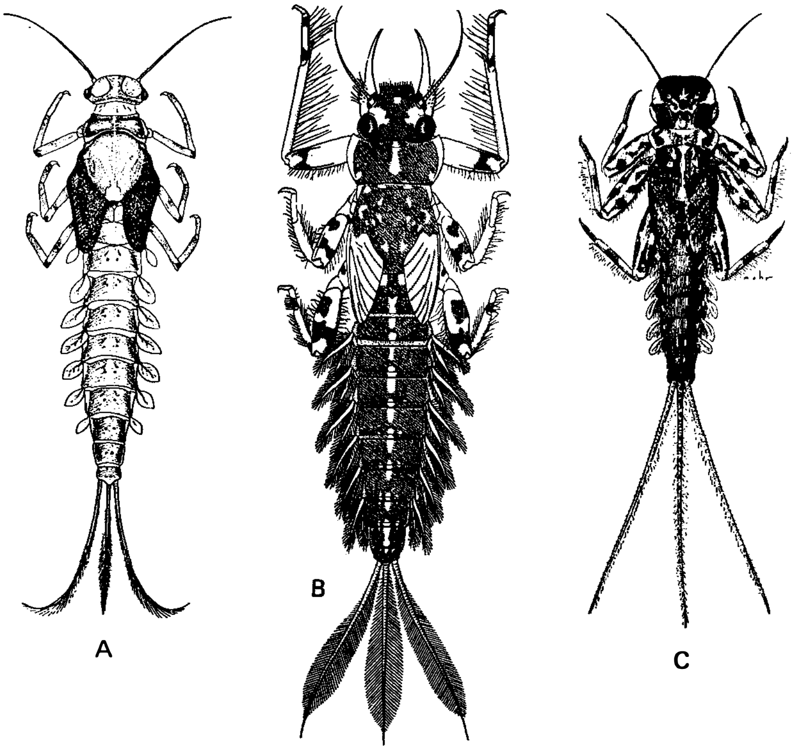


Figure 9–2 Mayfly nymphs. A, *Baetis brunneicolor* McDunnough (Baetidae); B, *Anthopotamus* sp. (Potamanthidae); C, *Heptagenia diabasia* Burks (Heptageniidae). (A, Courtesy of Leonard and the Entomological Society of America; B, Courtesy of Needham and the Bureau of Fisheries; C, Courtesy of Burks and the Entomological Society of America.)

curred along the shores of Lake Erie, but changes in the lake (increased pollution) have greatly reduced the number of these insects (and also the numbers of many fish), and their emergences now are not as striking as they used to be.

The chief economic importance of mayflies lies in their value as food for fish. Both adults and nymphs are an important food of many freshwater fish, and many artificial flies used by fishermen are modeled after these insects. Mayflies also serve as food for many other animals, including birds, amphibians, spiders, and many predaceous insects. Most species of mayflies in the nymphal stage are restricted to particular types of habitats. Hence the mayfly fauna of an aquatic habitat may serve as an indicator of the ecological characteristics (including the degree of pollution) of that habitat.

Some Characters of the Ephemeroptera

The head. The compound eyes often differ in the two sexes, being generally larger and closer together in the male, and smaller and farther apart in the female. In most of the smaller species, such as the Caenidae, the eyes are small and widely separated in both sexes. The eyes of the male are often larger or have upper facets that are a different color from the other facets. In the Baetidae and some Leptophlebiidae, the upper facets are more or less on stalks (such eyes are described as *turbinate*). The eyes of the female are usually uniform in color and facet size.

The legs. In most mayflies, the front legs of the male are much longer than the other legs (the tibiae and tarsi being much elongated), sometimes as long as or longer than the body. In the Polymitarcyidae and Behningiidae, the middle and hind legs of the male and all the legs of the female are vestigial.

The wings. Most mayflies have two pairs of wings, but in the Caenidae, Leptohyphidae, Baetidae, and some Leptophlebiidae the hind wings are greatly reduced or absent. The shape of the front wings is somewhat triangular in most mayflies, but the front wings are more elongate in those species that have reduced hind wings or lack them altogether. The wings are somewhat corrugated, with the veins lying either on a ridge or in a furrow. Some veins contain bullae, weakened areas that allow the wings to bend during flight.

There is considerable variation in the venational terminologies different authorities use in this group. We use here the terminology of Edmunds and Traver (1954a; Figure 9–3), which differs a little from that used by many earlier researchers. In addition, Kukalová-Peck (1985) proposed a reinterpretation of mayfly venation, bringing it in line with her hypotheses on the fundamental structure of pterygote wings. Table 9–1 presents a comparison of these three venational terminologies (veins labeled I are intercalaries).

The abdomen. The abdomen of a mayfly is 10-segmented, with the caudal filaments arising on the tenth segment. Some mayflies have only two caudal filaments (the cerci), with the median filament vestigial or absent; others have all three filaments well developed. The sternum of segment 9 forms the subgenital plate. The male has a pair of clasperlike genital forceps on the distal margin of this plate and paired penes (rarely, the penes are more or less fused) dorsal to this plate (Figure 9–5). The subgenital plate of the female, formed by the posterior part of the ninth sternum, varies in shape, and there are no claspers or penes. The character of the claspers is sometimes used in separating families, and both the claspers and the penes are usually very important in separating species.

Table 9–1 A Comparison of Venational Terminologies in the Ephemeroptera

Kukalová-Peck (1985)	Edmunds and Traver (1954a); Edmunds et al. (1976)[*]	Needham et al. (1935)[†]
C[‡]	C	C
ScP	Sc	Sc
RA	R_1	R_1
RP1	R_2	R_2
RP2	$R_{3(a+b)}$	
RP3–4	R_{4+5}	R_3
MA1–2	MA_1	R_4
	IMA	
MA3–4	MA_2	R_5
MP1–2	MP_1	M_1
	IMP	
MP3–4	MP_2	M_2
CuA1–2	CuA	Cu_1
Cu supplements + CuA3–4	Cubital intercalaries	Cu_1
CuP (+AA1)	CuP	Cu_2
AA2	1A	1A

[*] Used in this book and by many present workers on the Ephemeroptera.

[†] Used by Burks (1953) and in previous editions of this book.

[‡] The costal margin is formed by the fusion of PC, CA, CP, and ScA1–2; Sc3–4 forms the subcostal brace at the base of the wing (the costal brace of Edmunds & Traver 1954a).

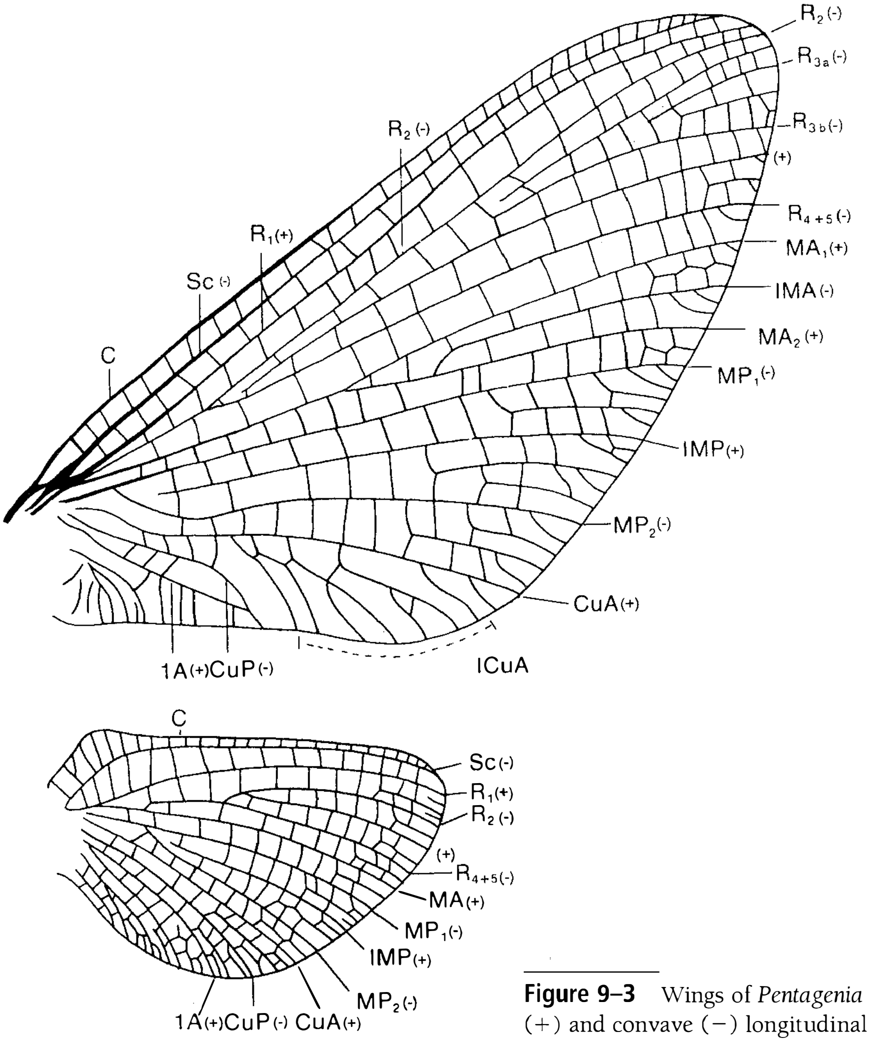


Figure 9-3 Wings of *Pentagenia* (Ephemeridae). Major convex (+) and convave (−) longitudinal veins indicated.

Classification of the Ephemeroptera

Several higher classifications have been proposed recently for Ephemeroptera, ranging from 0 to 4 suborders, and several more infraorders and superfamilies. The situation is presently in a state of active flux. The following list begins at the relatively stable level of family, and the names are simply listed in alphabetical order. The numbers of genera and species are from the 2002 list of the *Mayflies of North America* Web site. The groups marked with an asterisk are relatively rare or are unlikely to be taken by the general collector.

Acanthametropodidae (2): *Acanthametropus* (1), *Analetris* (1)
Ameletidae (34): *Ameletus* (34)
Ametropodidae (3): *Ametropus* (3)
Arthropleidae (1): *Arthroplea* (1)
Baetidae (135): *Acentrella* (6), *Acerpenna* (4), *Americabaetis* (3), *Apobaetis* (3), *Baetis* (22), *Baetodes* (6), *Baetopus* (1), *Barbaetis* (1), *Callibaetis* (12), *Camelobaetidius* (5), *Centroptilum* (15), *Cloeodes* (3), *Cloeon* (1), *Diphetor* (1), *Fallceon* (1), *Heterocloeon* (4), *Paracloeodes* (1), *Plauditus* (13), *Procloeon* (25), *Pseudocentroptiloides* (2), *Pseudocloeon* (6)
Baetiscidae (12): *Baetisca* (12)
Behningiidae (1): *Dolania* (1)
Caenidae (26): *Americaenis* (1), *Brachycercus* (10), *Caenis* (12), *Cercobrachys* (3)
Ephemerellidae (96): *Attenella* (4), *Caudatella* (7), *Caurinella* (1), *Dannella* (3), *Dentatella* (2), *Drunella* (15), *Ephemerella* (34), *Eurylophella* (15), *Serratella* (13), *Timpanoga* (2)
Ephemeridae (15): *Ephemera* (7), *Hexagenia* (5), *Litobrancha* (1), *Pentagenia* (2)

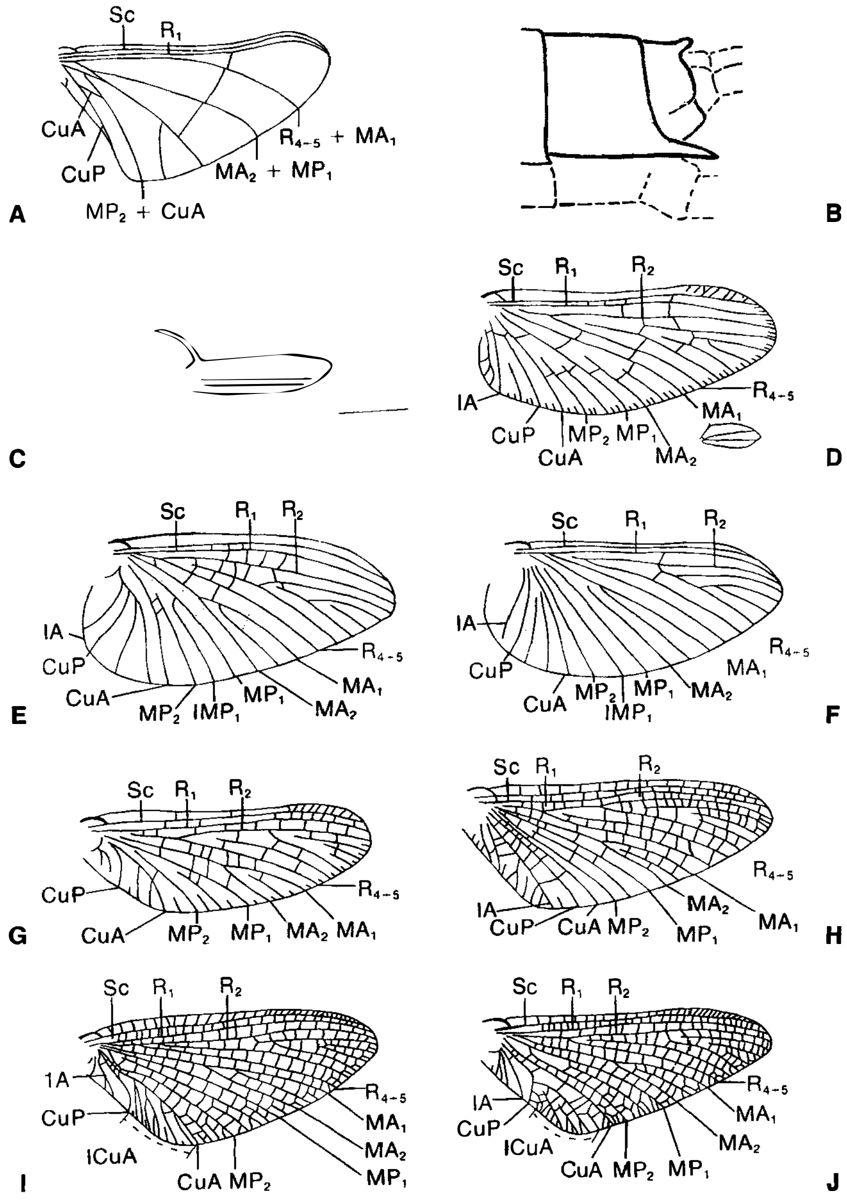


Figure 9–4 Wings of Ephemeroptera. A, *Lachlania*, Oligoneuriidae, front wing; B, *Neoephemera*, Neoephemeridae, terga 9 and 10; C, *Leptohyphes*, Leptohyphidae, hind wing of male; D, *Baetis*, Baetidae, front and hind wings; E, *Tricorythodes*, Leptohyphidae, front wing; F, *Caenis*, Caenidae, front wing; G, *Ephemerella*, Ephemerellidae, front wing; H, *Baetisca*, Baetiscidae, front wing; I, *Anthopotamus*, Potamanthidae, front wing; J, *Leptophlebia*, Leptophlebiidae, front wing.

Heptageniidae (127): *Acanthomola* (1), *Anepeorus* (2), *Cinygma* (3), *Cinygmula* (10), *Epeorus* (19), *Heptagenia* (12), *Ironodes* (6), *Leucrocuta* (10), *Macdunnoa* (3), *Nixe* (11), *Raptoheptagenia* (1), *Rhithrogena* (22), *Stenacron* (7), *Stenonema* (20)
Isonychiidae (16): *Isonychia* (16)
Leptohyphidae (25): *Allenhyphes* (2), *Asioplax* (5), *Homoleptohyphes* (3), *Leptohyphes* (2), *Tricoryhyphes* (1), *Tricorythodes* (10), *Vacupernius* (2)
Leptophlebiidae (66): *Choroterpes* (5), *Farrodes* (1), *Habrophlebia* (1), *Habrophlebiodes* (4), *Leptophlebia* (7), *Neochoroterpes* (3), *Paraleptophlebia* (39), *Thraulodes* (3), *Traverella* (3)
Metretopodidae (9): *Metretopus* (2), *Siphloplecton* (7)
Neoephemeridae (4): *Neoephemera* (4)
Oligoneuriidae (6): *Homoeoneuria* (4), *Lachlania* (2)
Polymitarcyidae (6): *Campsurus* (2), *Ephoron* (2), *Tortopus* (2)
Potamanthidae (5): *Anthopotamus* (5)
Pseudironidae (1): *Pseudiron* (1)
Siphlonuridae (24): *Edmundsius* (1), *Parameletus* (4), *Siphlonisca* (1), *Siphlonurus* (18)

Key to the Families of Ephemeroptera

The venational characters used are those of the front wing, unless otherwise indicated. This key is modified from the last edition of this book and Edmunds and Waltz (1996) by Manuel L. Pescador and Janice Peters. Groups marked with an asterisk (*) are relatively rare or are unlikely to be taken by the general collector. Keys to nymphs are given by Edmunds et al. (1963), Edmunds (1984), and Edmunds and Allen (1987).

1.	Fore wing venation appears reduced, with apparently only 3 or 4 longitudinal veins behind R_1 (Figure 9–4A)	Oligoneuriidae	p. 191
1′.	Fore wing venation complete or moderately reduced, with numerous longitudinal veins present behind R_1	2	
2(1′).	Bases of MP_2 and CuA of fore wing strongly divergent and recurved from MP_1 (Figures 9–3, 9–4I), or recurved base of MP_2 close to or fused with CuA (Figure 9–4D, H, J)	3	
2′.	Bases of MP_2 and CuA of fore wing little divergent from MP_1 (MP_2 only may diverge from MP_1) (Figures 9–6C,D)	7	
3(2).	Middle and hind legs of male and all legs of female atrophied (or lost) beyond trochanter; vein MA of fore wing forked in basal half (Figure 9–6A, B)	4	
3′.	All legs well developed in both sexes; vein MA of fore wing forked near middle of wing (Figures 9–3, 9–4I)	5	
4(3).	Males with penes twice as long as genital forceps; female wings white	Behningiidae*	p. 190
4′.	Males with penes shorter than genital forceps; female wings hyaline	Polymitarcyidae	p. 191
5(3′).	Abdominal tergum 9 with well-developed posterolateral projections with apex about as long as tergum 10; body robust	Neoephemeridae	p. 190
5′.	Lateral margins of abdominal tergum 9 without projections as in preceding entry; most species with slender body	6	
6(5′).	Vein 1A of fore wing forked near margin (Figure 9–4I)	Potamanthidae	p. 191
6′.	Vein 1A of fore wing unforked, but with three or more veinlets extending to hind margin of wing (Figure 9–3)	Ephemeridae	p. 190
7(2′).	Fore wing cubital intercalaries with a series of veinlets, often forked or sinuate, extending from CuA to hind margin of wing (Fig. 9–6D); vein MA of hind wing forked; hind wings present	8	
7′.	Fore wing cubital intercalaries not as in preceding entry; vein MA of hind wing forked or unforked; hind wing present, reduced, or absent	11	

8(7).	Three caudal filaments present, median filament distinctly longer than abdominal tergum 10; hind wing ½ or more length of fore wing; very rare	Acanthametropodidae*	p. 189
8′.	Two caudal filaments present, medial filament vestigial; hind wing less than ½ length of fore wing	9	
9(8′).	Vein MP of hind wing forked near margin; fore legs largely or entirely dark; middle and hind legs pale	Isonychiidae	p. 190
9′.	Vein MP of hind wing forked near base or middle of wing; legs not as in preceding entry	10	
10(9′).	Tarsal claws of each leg dissimilar, one pointed, the other rounded or padlike	Ameletidae	p. 189
10′.	Tarsal claws on each leg similar in form, pointed	Siphlonuridae	p. 191
11(7′).	Three well-developed caudal filaments present (median filament sometimes shorter and thinner than cerci)	12	
11′.	Two well-developed caudal filaments present (median filament rudimentary or absent)	15	
12(11).	Hind wings present, usually relatively large with one or more veins forked; costal projection of hind wings, if present, shorter than width of wing	13	
12′.	Hind wings absent or very small, with only 2 or 3 simple veins; costal projection of hind wings, if present, as long as or longer than width of wing	20	

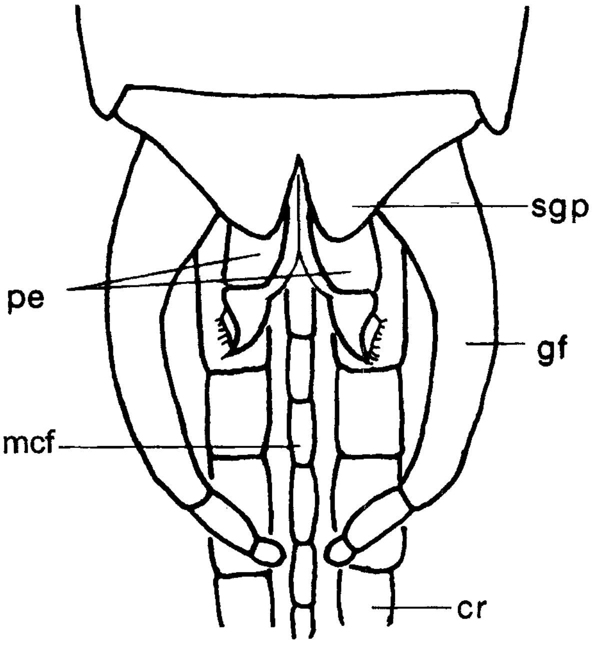


Figure 9–5 Apex of abdomen of male mayfly, *Leptophlebia cupida* (Say), ventral view. *cr*, lateral caudal filament (cercus); *gf*, genital forceps; *mcf*, median caudal filament; *pe*, penes; *sgp*, subgenital plate.

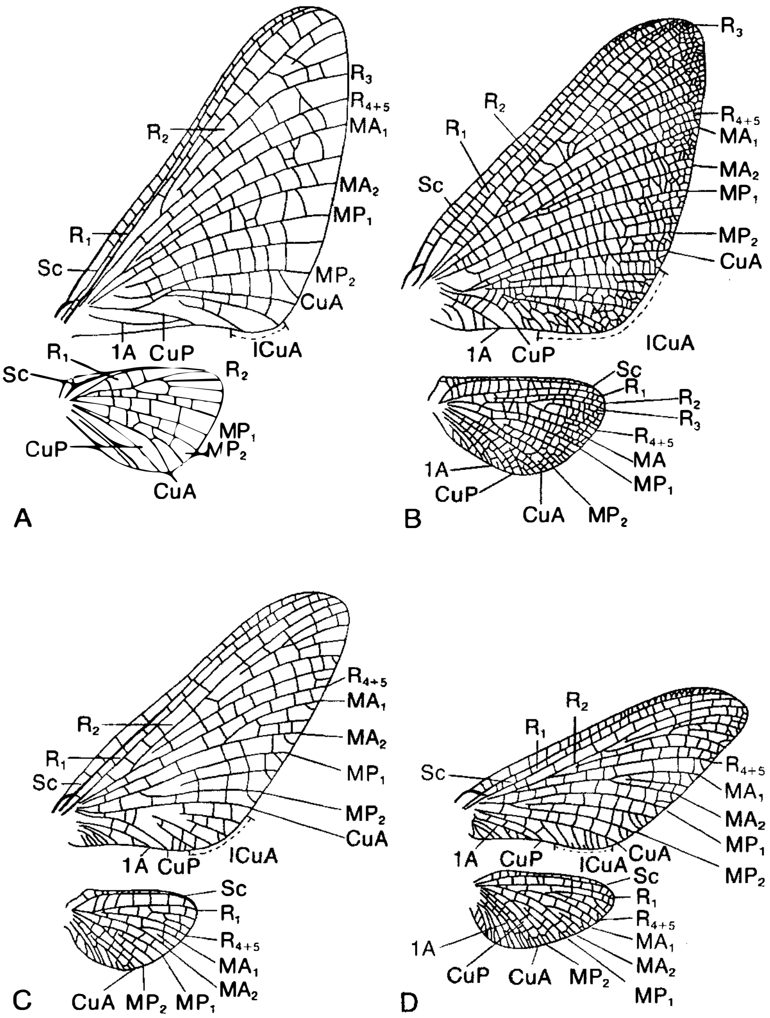


Figure 9–6 Wings of Ephemeroptera. A, *Campsurus*, Campsurinae, Polymitarcyidae; B, *Ephoron*, Polymitarcyinae, Polymitarcyidae; C, *Stenonema*, Heptageniidae; D, *Siphlonurus*, Siphlonuridae.

13(12). Fore wing with 1 long pair of parallel cubital intercalaries and several shorter intercalaries between CuA and CuP; vein 1A attached to hind margin of wing by series of marginal veinlets; western United States — Ametropodidae* p. 189

13′. Fore wing with cubital intercalaries not as in preceding entry; vein 1A not as in preceding entry; widely distributed — 14

14(13′). Fore wing with short, basally detached marginal veinlets along outer margin of wing; vein CuA basally close to or overlapping base of vein CuP (Figure 9–4G); genital forceps of male with one terminal segment — Ephemerellidae p. 190

14′. Fore wing without basally detached marginal veinlets along outer margin of wing; base of CuA separated from base of CuP (Figure 9–4J); male genital forceps with 2 or 3 terminal segments (Figure 9–5) — Leptophlebiidae p. 190

15(11′). Cubital intercalaries absent in fore wing and vein 1A extending to outer margin of wing (Figure 9–4H); hind wing with numerous long, free marginal veinlets — Baetiscidae p. 190

15′. Cubital intercalaries present in fore wing and vein 1A extending to hind margin of wing (Figures 9–4D, 9–6C); hind wing (if present) not as in preceding entry — 16

16(15′).	Fore wing with 1 or 2 short, basally detached marginal veinlets between main longitudinal veins; bases of veins MA$_2$ and MP$_2$ detached from their respective stems (Figure 9–4D); 1 long and 1 short cubital intercalary present (Figure 9–4D); hind wing small or absent; upper portion of male eye large and on stalk	Baetidae	p. 190
16′.	Fore wing with marginal intercalaries attached basally to other veins (Figure 9–6C); bases of veins MA$_2$ and MP$_2$ attached to MA$_1$ and MP$_1$; usually with 2 pairs (rarely 1) of cubital intercalaries (Figure 9–6C); hind wings relatively large; male eyes not on stalks	17	
17(16′).	Hind tarsi distinctly 5-segmented	18	
17′.	Hind tarsi apparently 4-segmented, basal segment more or less fused to tibia	19	
18(17).	Genital forceps of male with 3 short terminal segments; MA of hind wing unforked; rare, U.S. Northeast west to Wisconsin	Arthropleidae*	p. 189
18′.	Genital forceps of male with 2 short terminal segments; MA of hind wing usually forked (Figure 9–6C); very common, widespread	Heptageniidae	p. 190
19(17′).	Eyes of male imago separated by distance greater than width of median ocellus; length of fused basal segment of hind tarsus less than ½ length of tibia; subgenital plate of female with median cleft; abdominal sterna without median marks	Pseudironidae*	p. 191
19′.	Eyes of male imago contiguous (touching) medially or nearly so; length of fused basal segment of hind tarsus greater than ½ length of tibia; subgenital plate of female evenly rounded; abdominal sterna with median dots or lines	Metretopodidae	p. 190
20(12′).	Veins MP$_2$ and IMP of fore wing extending less than ¾ distance to base of wing (Figure 9–4E); male genital forceps 2- or 3-segmented; hind wings present or absent; thorax usually black or gray	Leptohyphidae	p. 190
20′.	Veins MP$_2$ and IMP of fore wing extending nearly to base of wing (Figure 9–4F); male genital forceps 1-segmented; hind wings absent; thorax color variable, usually brown	Caenidae	p. 190

Family **Acanthametropodidae:** Two genera of these rare and sporadically distributed mayflies are known from North America, but only one has been collected as an adult. They have relatively large hind wings with their length one half or more of the length of the fore wing, and three caudal filaments with the median filament distinctly longer than abdominal tergum 10. The nymphs have long, slender tarsal claws (especially the hind tarsal claws) that enable them to maintain their position in sandy bottom streams.

Family **Ameletidae:** The adults are similar to Siphlonuridae, from which they are distinguished by the dissimilarity of the tarsal claws on each leg: one pointed and the other rounded or padlike. The fast-swimming nymphs inhabit a wide variety of habitats, ranging from swift-flowing streams to large rivers, lakes, and ponds. They occur mostly among pebbles on gravelly substrates, although a few nymphs have been collected among vegetation and debris.

Family **Ametropodidae:** These mayflies have a wing venation similar to that of the Heptageniidae (Figure 9–6C), but they have three caudal filaments (two in the Heptageniidae), and the hind tarsi have four segments. The nymphs live buried in the silty sand in the bottoms of large rivers with a fairly strong current.

Family **Arthropleidae:** Adults are similar to Heptageniidae, but the genital forceps of the males have three short terminal segments and vein MA of the hind wing is unforked. The family is represented by one rare, widely distributed species, *Arthroplea bipunctata* (McDunnough). The nymphs live on vegetation in temporary ponds and marginal areas of streams and feed by sweeping elongate maxillary palpi through the water.

Family **Baetidae:** This is the largest family of mayflies in North America, and its members are common and widely distributed. The nymphs occur in a variety of aquatic habitats. The adults are small (front wings 2–12 mm), with front wings elongate-oval and hind wings very small or absent. Baetids (Figure 9–4D) differ from other mayflies that have hind wings small or absent (Caenidae, Figure 9–4F; Leptohyphidae, Figure 9–4E; and some Leptophlebiidae) in having only two caudal filaments, one or two short marginal veinlets between the main longitudinal veins, and the bases of MA_2 and MP_2 atrophied. The eyes of the male are divided, with the upper portion turbinate.

Family **Baetiscidae:** These mayflies are small to medium-sized (front wing 8–12 mm), with two caudal filaments (which are usually shorter than the body). The wings are often reddish or orange, at least basally. The front wing lacks cubital intercalaries and has 1A extending to the outer margin of the wing (Figure 9–4H). The nymphs occur principally in cool, fairly rapid streams.

Family **Behningiidae:** This group is represented in the United States by a single rare species. *Dolania americana* Edmunds and Traver, which has been found in the southeastern states with one record from Wisconsin. The nymphs burrow in the sand at the bottom of large rivers.

Family **Caenidae:** These mayflies are quite small (front wing 2–6 mm), with three caudal filaments and no hind wings. They are similar to the Leptohyphidae, but the fork of MA is asymmetrical and veins IMP_1 and MP_2 extend nearly to the wing base (Figure 9–4F). The nymphs occur in a variety of aquatic habitats, usually in quiet water.

Family **Ephemerellidae:** These mayflies are medium-sized (front wing 6–19 mm) and usually brownish, with three caudal filaments. They have short, basally detached marginal veinlets along the outer margin of the front wing, and the costal crossveins are reduced (Figure 9–4G). The ephemerellids are common and widely distributed mayflies. The nymphs live in a variety of aquatic habitats, usually under rocks or in debris in cool, clear, rapid streams or in small, clear lakes.

Family **Ephemeridae:** These mayflies are medium-sized to large (front wings 10–25 mm), with two or three caudal filaments. The wings are hyaline or brownish and, in *Ephemera*, have dark spots. The nymphs are burrowing in habit and occur in the sand or silt at the bottoms of streams and lakes, sometimes in fairly deep water. Adults of *Hexagenia* (Figure 9–1) sometimes emerge from lakes in tremendous numbers.

Family **Heptageniidae:** This is the second largest family of mayflies in North America, and its members are common and widely distributed. The nymphs are sprawling forms, sometimes dark-colored, with the head and body flattened (Figure 9–2C). Most species occur on the underside of stones in streams, but some occur in sandy rivers and boggy ponds. Adults have two caudal filaments and two pairs of cubital intercalaries that are more or less parallel (Figure 9–6C), and MA in the hind wing is usually forked. The hind tarsi are five-segmented.

Family **Isonychiidae:** The adults are easily recognized by the forked vein MP of the hind wings near the wing margin, and the largely or entirely dark fore legs and pale middle and hind legs. The minnowlike nymphs are mostly found in flowing water with rapid current, from which they filter food particles through the double row of long hairs on the fore tibiae and femora.

Family **Leptohyphidae:** This group is largely tropical, but a few species extend into Canada. The nymphs occur in rivers and streams. The adults are small (front wing 3–9 mm), with three caudal filaments. The front wings are elongate-oval or wider at the base, without marginal veinlets. MA forms a symmetrical fork and MP_2 is usually free at its base (Figure 9–4E). Hind wings are lacking, but males of some genera have small hind wings with a long, slender costal projection (Figure 9–4C).

Family **Leptophlebiidae:** This is a fairly large group, and its members are relatively common and widely distributed. The nymphs occur in a variety of aquatic habitats, usually in still water or in streams with a reduced current. Adults have three caudal filaments, and the venation (Figure 9–4J) is fairly complete. There are no detached veinlets, and CuP is rather strongly recurved. The eyes of the male are strongly divided, with the upper portion having larger facets. Adults range in size (measured by the length of the front wing) from 4 to 14 mm.

Family **Metretopodidae:** The nymphs of this small group generally live in large, slowly flowing streams, usually in shallow water near the shore. The adults have a wing venation similar to that of the Heptageniidae (Figure 9–6C), but the hind tarsi are four-segmented (five-segmented in the Heptageniidae). These mayflies are chiefly northern in distribution, occurring across Canada to the U.S. Southeast.

Family **Neoephemeridae:** These mayflies are similar to the ephemerids, but they have somewhat reduced costal crossveins and an acute costal projection near the base of the hind wing. They are easily recognized by the acute lateral projections on abdominal tergum 9 (9–4B). The nymphs live in slow to moderately rapid streams, usually in debris. This is a small group whose members occur in the eastern United States. They are not very common.

***Family* Oligoneuriidae:** The adults of genera in this family have greatly reduced wing venation (Figure 9–4A). The nymphs live in fairly rapid streams clinging to rocks or vegetation (*Lachlania*) or partially burrowed in sand (*Homoeoneuria*).

***Family* Polymitarcyidae:** These mayflies are similar to the Ephemeridae, but have the middle and hind legs of the male, and all legs of the female, greatly reduced or vestigial. They are widely distributed but not very common. Some (Polymitarcyinae) have a dense network of marginal veinlets (Figure 9–6B), and the genital forceps of the male have four segments. Others (Campsurinae) have few marginal veinlets (Figure 9–6A), and the genital forceps of the male have two segments.

***Family* Potamanthidae:** The nymphs of this group live in the silt or sand at the bottom of swiftly flowing shallow water. The adults are pale in color, with the vertex and thoracic dorsum reddish brown, and the front wings are 7–13 mm in length. There are three caudal filaments, and the median filament is a little shorter than the lateral ones. The wing venation is similar to that of the Ephemeridae, but 1A is forked near the wing margin (Figure 9–4I).

***Family* Pseudironidae:** Adults of this monogeneric family are similar to Heptageniidae, but have only four free tarsal segments. The length of the fused basal segment of the hind tarsus is less than half the length of the hind tibia. The nymphs have spiderlike long legs and are found in sand rivers over much of North America. The nymphs have mouthparts adapted for predation with the mandibular incisors modified apically and equipped with sharp, pointed spines. Only one species, *Pseudiron centralis* McDunnough, occurs in the United States.

***Family* Siphlonuridae:** The nymphs of these mayflies are streamlined in form and occur principally in rapidly flowing streams and rivers. At least some are predaceous on tube-dwelling midge larvae and other small aquatic insects. The adults resemble the Heptageniidae in having MA in the hind wing forked, but they do not have two parallel pairs of cubital intercalaries (compare Figure 9–6C,D), and the hind tarsi are four-segmented (five-segmented in the Heptageniidae). This is a large and widely distributed group, and its members vary in size (measured by the length of the front wings) from 8 to 20 mm.

Collecting and Preserving Ephemeroptera

Most adult mayflies are captured with a net, either from swarms or by sweeping vegetation. One sometimes needs a net with a very long handle for swarms high above the ground. Some mayflies may be taken at night at lights, especially when the nights are warm and the sky is overcast. Large numbers of adults can sometimes be obtained with a trap such as a Malaise trap (Figure 35–5C). Curtains of netting placed over a stream can serve as a surface on which emerging mayflies alight and from which they can be collected.

If subimagos are collected (usually recognizable by their dull appearance and pubescence), allow them to molt to the adult stage. This is done by transferring them to small boxes (without actually handling them if possible, as they are very delicate). A cardboard box with a clear plastic window is good for this purpose.

Adults of many species are best obtained by rearing them from nymphs, in a container where the adults can be captured. Nymphs with black wing pads are nearly mature and are the best to select for rearing, because they usually transform to the winged stage in a day or two. When the subimago emerges, transfer it to a box where it can molt to the adult stage.

Mayfly nymphs can be collected in various types of aquatic habitats by the methods of collecting aquatic insects.

Adult mayflies are extremely fragile and must be handled with considerable care. They can be preserved dry, on pins or points or in paper envelopes, or in alcohol. Specimens preserved dry retain their color better than those preserved in alcohol, but they sometimes become somewhat shriveled and are more subject to breakage. Adults preserved in alcohol should be preserved in 80% alcohol, preferably with 1% of ionol added.

Nymphs are best put directly into modified Carnoy fluid (glacial acetic acid, 10%; 95% ethanol, 60%; chloroform, 30%). After a day or so, drain off the Carnoy fluid and replace it with 80% alcohol. A good substitute for Carnoy fluid is Kahle's fluid (formalin, 11%; 95% ethanol, 28%; glacial acetic acid, 2%; water, 59%). In about a week drain this fluid off and replace it with 80% alcohol. If neither Carnoy nor Kahle's fluid is available, nymphs can be preserved in 95% alcohol.

References

Allen, R. K., and G. F. Edmunds, Jr. 1965. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VIII. The subgenus *Ephemerella* in North America. Misc. Publ. Entomol. Soc. Amer. 4:244–282.

Bae, Y., and W. P. McCafferty. 1991. Phylogenetic systematics of the Potamanthidae (Ephemeroptera). Trans. Amer. Entomol. Soc. 117:1–143.

Bae, Y. J., and W. P. McCafferty. 1998. Phylogenetic systematics and biogeography of the Neoephemeridae (Ephemeroptera: Pannota). Aquatic Insects 20:35–68.

Bednarik, A. F., and W. P. McCafferty. 1979. Biosystematic revision of the genus *Stenonema* (Ephemeroptera: Heptageniidae). Can. Bull. Fish. & Aquatic Sci. 201. 73 pp.

Berner, L. 1978. A review of the family Metretopodidae. Trans. Amer. Entomol. Soc. 104:91–137.

Berner, L., and M. L. Pescador. 1988. The Mayflies of Florida (rev. ed.). Gainesville: University of Florida Press, 415 pp.

Brittain, J. E. 1982. Biology of mayflies. Annu. Rev. Entomol. 27:119–147.

Burian, S. K. 2001. A revision of the genus *Leptophlebia* Westwood in North America (Ephemeroptera: Leptophlebiidae: Leptophlebiinae). Bull. Ohio Biol. Surv. n.s. 13(3). 80 pp.

Burks, B. D. 1953. The mayflies of Ephemeroptera of Illinois. Bull. Ill. Nat. Hist. Surv. 26:1–216.

Day, W. C. 1956. Ephemeroptera. In R. L. Usinger (Ed.), Aquatic Insects of California. Berkeley: University of California Press, pp. 79–105.

Edmunds, G. F., Jr. 1962. The type localities of the Ephemeroptera of North America north of Mexico. Univ. Utah Biol. Ser. 12(5):1–39.

Edmunds, G. F., Jr. 1972. Biogeography and evolution of the Ephemeroptera. Annu. Rev. Entomol. 17:21–42; illus.

Edmunds, G. E, Jr. 1984. Ephemeroptera. In R. W. Merritt and K. W. Cummins (Eds.), An introduction to the aquatic insects of North America, 2nd ed., pp. 94–123. Dubuque, IA: Kendall/Hunt.

Edmunds, G. F., Jr., and R. K. Allen. 1987. Order Ephemeroptera. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 75–94. Dubuque, IA: Kendall/Hunt, 754 pp.

Edmunds, G. F., Jr., R. K. Allen, and W. L. Peters. 1963. An annotated key to the nymphs of the families and subfamilies of mayflies (Ephemeroptera). Univ. Utah Biol. Ser. 13(1):1–49.

Edmunds, G. F., Jr., S. L. Jensen, and L. Berner. 1976. The Mayflies of North and Central America. Minneapolis: University of Minnesota Press, 300 pp.

Edmunds, G. F., Jr., and J. R. Traver. 1954a. The flight mechanics of the wings of Ephemeroptera with notes on the archetype wing. J. Wash. Acad. Sci. 44(12):390–400.

Edmunds, G. F., Jr., and J. R. Traver. 1954b. An outline of a reclassification of the Ephemeroptera. Proc. Entomol. Soc. Wash. 56:236–240.

Edmunds, G. F., Jr., and R. D. Waltz. 1996. Ephemeroptera. In R. W. Merrit and K. W. Cummins (Eds.), An introduction to the aquatic insects of North America, 3rd ed., Chapter 11, pp. 126–136. Dubuque, IA: Kendall Hunt.

Funk, D. H., and B. W. Sweeney. 1994. The larvae of eastern North American *Eurylophella* Tiensuu (Ephemeroptera: Ephemerellidae). Trans. Amer. Entomol. Soc. 120:209–286.

Hubbard, M. D. 1990. Mayflies of the world: A catalog of the family and genus group taxa. Gainesville, FL: Sandhill Crane Press, 119 pp.

Hubbard, M. D., and W. L. Peters. 1976. The number of genera and species of mayflies (Ephemeroptera). Entomol. News 87:245.

Kondratieff, B. C., and J. R. Voshell, Jr. 1984. The North and Central American species of *Isonychia* (Ephemeroptera: Oligoneuriidae). Trans. Amer. Entomol. Soc. 110:129–244.

Kukalová-Peck, J. 1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects. Can. J. Zool. 63:933–955.

Leonard, J. W., and F. A. Leonard. 1962. Mayflies of Michigan Trout Streams. Bloomfield Hills, MI: Cranbrook Institute of Science, 137 pp.

McCafferty, W. P. 1975. The burrowing mayflies (Ephemeroptera: Ephemeroidea) of the United States. Trans. Amer. Entomol. Soc. 101:447–504.

McCafferty, W. P. 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): A commentary on systematics. Ann. Entomol. Soc. Amer. 84:343–360.

McCafferty, W. P. 1996. The Ephemeroptera species of North America and index to their complete nomenclature. Trans. Amer. Entomol. Soc. 122:1–54.

McCafferty, W. P. 1998. Additions and corrections to Ephemeroptera species of North America and index to their complete nomenclature. Entomol. News 109:266–268.

McCafferty, W. P., and G. F. Edmunds, Jr. 1979. The higher classification of the Ephemeroptera and its evolutionary basis. Ann. Entomol. Soc. Amer. 72:5–12; illus.

McCafferty, W. P., and R. D. Waltz. 1990. Revisionary synopsis of the Baetidae (Ephemeroptera) of North and Middle America. Trans. Amer. Entomol. Soc. 116:769–799.

McCafferty, W. P., and T.-Q. Wang. 2000. Phylogenetic systematics of the major lineages of the pannote mayflies (Ephemeroptera: Pannota). Trans. Amer. Entomol. Soc. 126:9–101.

Morihara, D. K., and W. P. McCafferty. 1979. The *Baetis* larvae of North America (Ephemeroptera: Baetidae). Trans. Amer. Entomol. Soc. 105:139–221.

Needham, J. G., J. R. Traver, and Y.-C. Hsu. 1935. The biology of mayflies, with a systematic account of North America species. Ithaca, NY: Comstock, 759 pp.

Peckarsky, B. L., P. R. Fraissinet, M. A. Penton, and D. J. Conklin, Jr. 1990. Freshwater macroinvertebrates of northeastern United States. Ithaca, NY: Cornell University Press, 442 pp.

Pescador, M. L., and L. Berner. 1981. The mayfly family Baetiscidae (Ephemeroptera). Part II. Biosystematics of the genus *Baetiscas*. Trans. Amer. Entomol. Soc. 107:163–228.

Peters, W. L., and G. F. Edmunds, Jr. 1970. Revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera). Pac. Insects 12(1):157–240.

Provonsha, A. V. 1990. A revision of the genus *Caenis* in North America (Ephemeroptera: Caenidae). Trans. Amer. Entomol. Soc. 116:801–884.

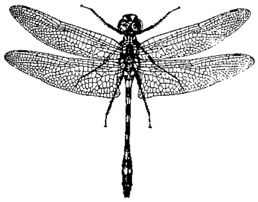
Soldán, T. 1986. A revision of the Caenidae with ocellar tubercles in the nymphal stage (Ephemeroptera). Acta Univ. Carl. 1982–1984 (Biol.):289–362.

Wiersema, N. A., and W. P. McCafferty. 2000. Generic revision of the North and Central American Leptohyphidae (Ephemeroptera: Pannota). Trans. Amer. Entomol. Soc. 126:337–371.

Zloty, J. 1996. A revision of the Nearctic *Ameletus* mayflies based on adult male, with descriptions of seven new species (Ephemeroptera: Ameletidae). Can. Entomol. 128:293–346.

10

Order Odonata[1,2]
Dragonflies and Damselflies



The Odonata are relatively large and often beautifully colored insects that spend a large part of their time on the wing. The immature stages are aquatic, and the adults are usually found near water. All stages are predaceous and feed on various insects and other organisms and, from the human point of view, are generally very beneficial. The adults are harmless to people; that is, they do not bite or sting. Certain groups are useful as indicators of ecosystem quality.

Adult dragonflies and damselflies are easily recognized (see Figures 10–10 through 10–14). The compound eyes are large and multifaceted, and often occupy most of the head. There are three ocelli. The antennae are very small and bristlelike, and the mouthparts are of the chewing type. The thorax consists of a small prothorax and a larger pterothorax. The dorsal and lateral surfaces of the pterothorax, between the pronotum and the base of the wings, are formed by pleural sclerites. The four wings are elongate, many-veined, and membranous. The legs are relatively long and suited for perching and holding prey, not for walking. The abdomen is long and slender, with 10 visible segments. The cerci are not segmented. Metamorphosis is simple.

Present-day Odonata vary in length from about 20 to more than 135 mm. The largest dragonfly known, which lived about 250 million years ago and is known only from fossils, had a wingspread of about 71 cm (28 inches)! The largest dragonflies in the United States are about 85 to 115 mm in length, although they often look much larger when seen on the wing.

Odonata nymphs are aquatic and breathe through the general integument, with gaseous exchange supplemented by gills. The gills of damselfly nymphs (Zygoptera) are in the form of three leaflike structures at the end of the abdomen (Figure 10–1). These nymphs swim by body undulations, the gills functioning like the tail of a fish. The gills of dragonfly nymphs (Anisoptera) (Figures 10–2 and 10–11A,B) are in the form of ridges in the rectum. When a dragonfly nymph breathes, it draws water into the rectum through the anus and then expels it. Rapid expulsion of water from the anus is a chief means of locomotion, resulting in a form of "jet propulsion."

The nymphs vary somewhat in habits, but all are aquatic and feed on various sorts of small aquatic organisms. They usually lie in wait for their prey, either on a plant or more or less buried in the substrate. The prey is generally small, but some of the larger nymphs (particularly Aeshnidae) occasionally attack tadpoles and small fish. In the nymphs, the labium is modified into a peculiar segmented structure with which they capture prey. The labium is folded under the head when not at rest. When used, it is thrust forward very quickly, and the prey is grabbed by two movable, claw-like lobes (the palpi) at the tip of the labium (Figure 10–3). The labium, when extended, is usually at least a third as long as the body (Figure 10–11B).

Nymphs may molt 9 to 17 times, but the norm is 9 to 13. When a nymph is fully grown, it crawls up out of the water to complete its metamorphosis, usually on a plant stem or rock and usually early in the morning. The nymphs of some species wander many meters from the water before molting to the adult stage. Once out of the last nymphal skin, the adult expands to its full size in about 30 to 60 minutes. The flight of newly emerged

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[1] Odonata: from the Greek, meaning tooth (referring to the teeth on the mandibles).

[2] This chapter edited by K. J. Tennessen.

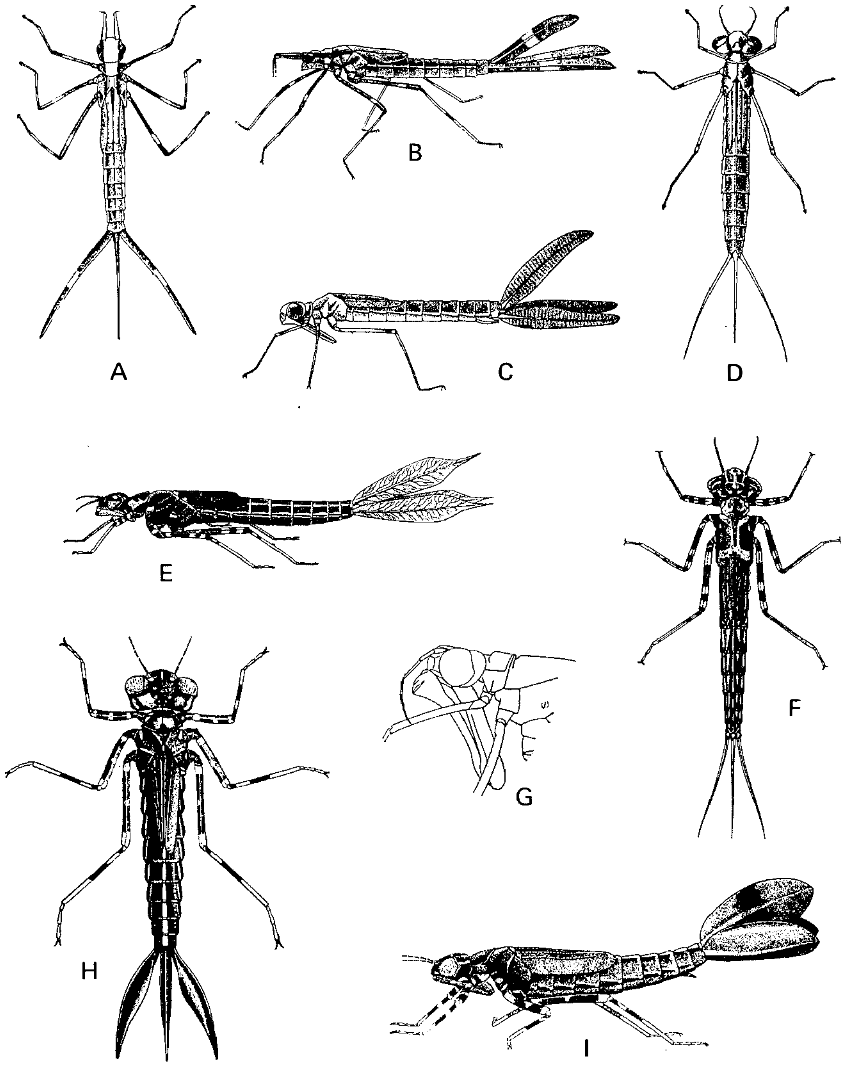


Figure 10–1 Nymphs of damselflies (Zygoptera), dorsal and lateral views. A and **B**, *Calopteryx aequabilis* (Say) (Calopterygidae); C and **D**, *Lestes dryas* Kirby (Lestidae); E and F, *Ischnura cervula* Selys (Coenagrionidae); G, head of *Lestes dryas*, lateral view; H and I, *Argia emma* Kennedy (Coenagrionidae). (Courtesy of Kennedy and the U.S. National Museum).

adults is relatively feeble, and they are not yet fully colored and are very soft-bodied. It is usually a few days before the insect's full powers of flight develop, and a week or more may elapse before the color pattern fully develops. Many Odonata have a color or color pattern in the first few days of their adult life that is quite different from what they will have after a week or two. Newly emerged, pale, soft-bodied adults are called *teneral* individuals.

The two sexes in the suborder Anisoptera are usually similarly colored, although the colors of the males are frequently brighter. In some of the Libellulidae, the two sexes differ in the color pattern of the wings or abdomen. The two sexes are differently colored in most of the Zygoptera, and the male is usually the more brightly colored, especially in the Coenagrionidae. Females of several genera within this family are polymorphic. For example, most females of *Ischnura verticalis* (Say) are heterochromatic, being orange and black when newly emerged and rather uniformly bluish when mature. A small proportion of the female population is homeochromatic.

Some species of Odonata are on the wing for only a few weeks each year, whereas others may be seen throughout the summer or over a period of several months. Observations of marked individuals indicate that the average damselfly probably has a maximum adult life of 3 or 4 weeks, and some dragonflies may live 6 to 10 weeks. Most species have a single generation a year, with the egg or, usually, the nymph over-

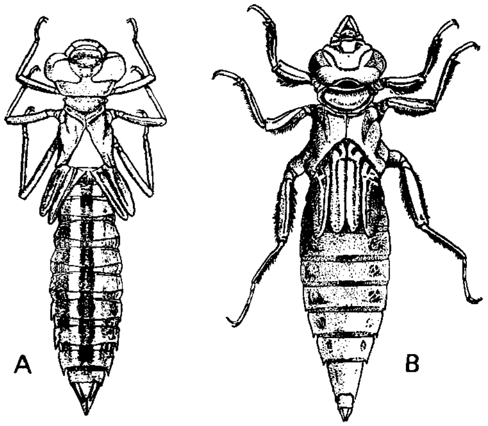


Figure 10–2 Nymphs of Aeshnoidea. A, *Aeshna verticalis* Hagen (Aeshnidae); B, *Gomphus quadricolor* Walsh (Gomphidae). (Courtesy of Walker and The Canadian Entomologist.)

wintering. A few of the larger darners and clubtails are known to spend two or more years in the nymphal stage.

Dragonflies and damselflies are peculiar among insects in having the copulatory organs of the male located at the anterior end of the abdomen, on the ventral side of the second and third segments. The male genitalia of other insects are located at the posterior end of the abdomen. The copulatory organs of male Odonata are therefore considered "secondary genitalia." Before mating, male Odonata must transfer sperm from the genital opening on the ninth segment to the penis, an extension of the third abdominal sternum that lies in the genital pocket of the second segment. This transfer is accomplished by bending the abdomen downward and forward.

The two sexes frequently spend considerable time "in tandem," with the male clasping the female by the back of the head or the prothorax with the appendages at the end of his abdomen. Copulation is usually initiated in flight, with the female bending her abdomen downward and forward and making contact with the secondary genitalia of the male. This coupling is known as the "wheel position." In all Zygoptera and many Anisoptera, the pair perches to finish copulation. In most Libellulidae, copulation is brief and occurs in flight.

Odonata lay their eggs in or near water and may do so while in tandem or when alone. In some species where the female detaches from the male before beginning oviposition, the male remains nearby "on guard" while the female is ovipositing and chases off other males that come near. This is known as "noncontact guarding." An unprotected female, after she begins ovipositing, may be interrupted by another male, who may grab and fly off in tandem with her. Males of most species of Odonata can displace the sperm from a previous mating within the female's spermatheca, a form of sperm competition (Waage 1984). Eggs are not fertilized during copulation, but during oviposition. Therefore, males that stay with their ovipositing mate have a better chance of ensuring that their genes pass on to the next generation.

Females of the Gomphidae, Corduliidae, and Libellulidae do not have an ovipositor, and the eggs are generally laid on the surface of the water by the female flying low and dipping her abdomen in the water and washing off the eggs. The females of most species in these groups oviposit alone. A somewhat rudimentary ovipositor is developed in the Cordulegastridae, which oviposit by hovering above shallow water with the body in a more or less vertical position and repeatedly jabbing the abdomen into the water and laying the eggs on the bottom of the body of water. The females of the other groups (Aeshnidae, Petaluridae, and all Zygoptera) have a well-developed ovipositor (Figure 10–4E) and insert their eggs in plant tissues (in many species

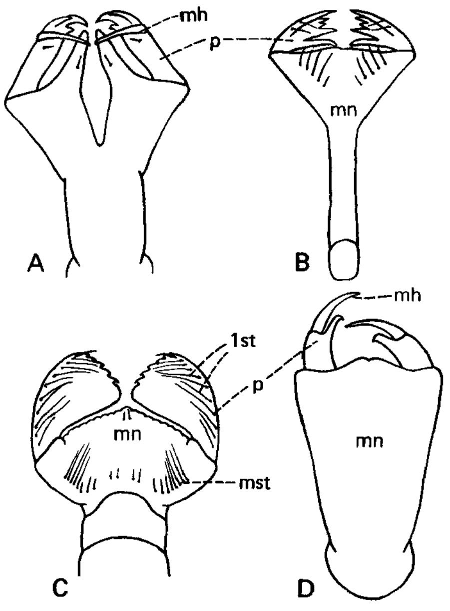


Figure 10–3 Labia of nymphal Odonata. A, *Calopteryx* (Calopterygidae); B, *Lestes* (Lestidae); C, *Plathemis* (Libellulidae); D, *Anax* (Aeshnidae). *lst*, lateral setae; *mh*, movable hook or palp; *mn*, mentum; *mst*, mental setae; *p*, palp or lateral lobe. (Redrawn from Garman.)

while still in tandem with the male). The eggs are usually inserted just below the surface of the water, no farther than the female can reach. In a few cases (for example, some species of *Lestes*), the eggs are laid in plant stems above the water line, and in a few other cases (for example, some species of *Enallagma*) the female may climb down a plant stem and insert her eggs into the plant a foot or more below the surface of the water. The eggs usually hatch in one to three weeks. In some species (for example, *Lestes*), however, the eggs overwinter and hatch the following spring.

Most species of Odonata have characteristic habits of flight. The flight of most skimmers (Libellulidae) is very erratic. They fly this way and that, often hovering in one spot for a few moments, and they seldom fly very far in a straight line. Many stream species fly relatively slowly up and down the stream, often patrolling a stretch of 90 meters or more. These dragonflies fly at

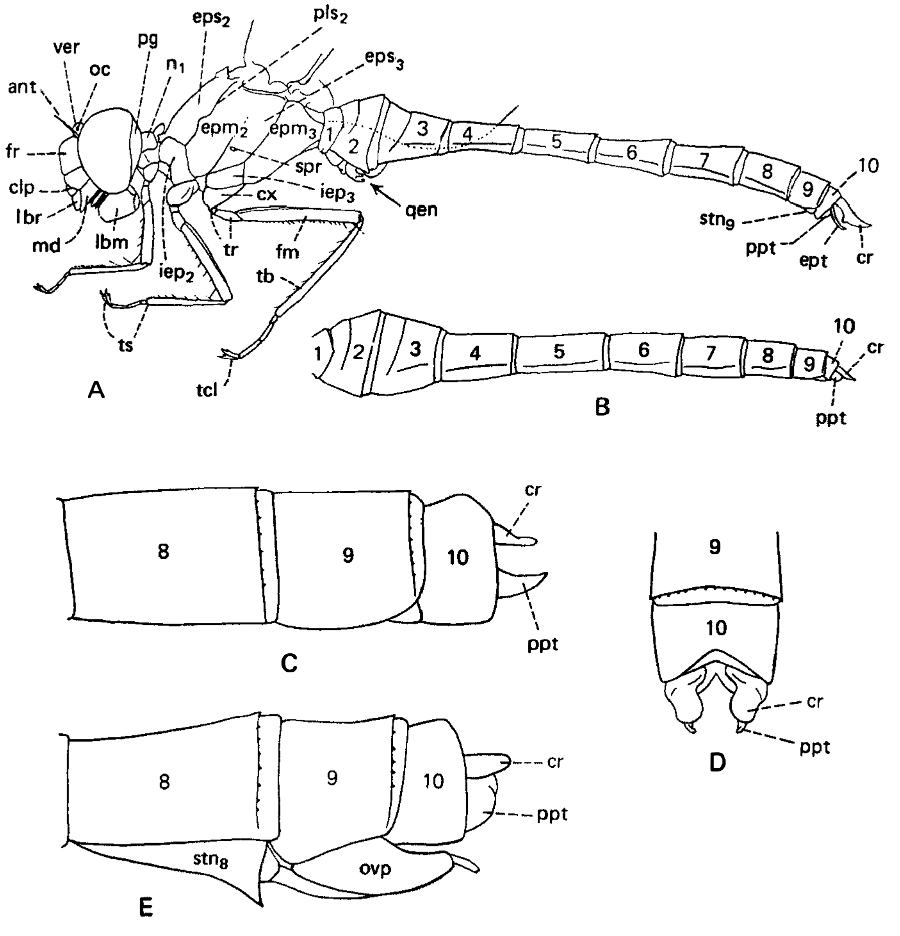


Figure 10–4 Structural characters of Odonata. A, Lateral view of *Sympetrum internum* Montgomery, male; B, Lateral view of abdomen of *S. internum*, female; C, Terminal abdominal segments of *Enallagma hageni* (Walsh), male lateral view; D, Same, dorsal view; E, Terminal abdominal segments of *E. hageni*, female, lateral view. *ant*, antenna; *clp*, clypeus; *cr*, cerci; *cx*, coxa; *e*, compound eye; *epm*$_2$, mesepimeron; *epm*$_3$, metepimeron; *eps*$_2$, mesepisternum; *eps*$_3$, metepisternum; *ept*, epiproct; *fm*, femur; *fr*, frons; *gen*, male copulatory apparatus; *iep*$_2$, mesinfraepisternum; *iep*$_3$, metinfraepisternum; *lbm*, labium; *lbr*, labrum; *md*, mandible; *n*$_1$, pronotum; *oc*, ocellus; *ovp*, ovipositor; *pg*, postgena; *pls*$_2$, mesopleural suture (or humeral suture); *ppt*, paraproct; *spr*, spiracle; *stn*, sternum; *tb*, tibia; *tcl*, tarsal claws; *tr*, trochanter; *ts*, tarsus; *ver*, vertex; *1–10*, abdominal segments.

a height and a speed that are characteristic for the species. Some of the gomphids, when flying over open land areas, fly with a very undulating flight, each undulation covering 1.2 to 1.8 meters vertically and 0.6 to 0.9 meters horizontally. Many of the corduliids and aeshnids fly from 1.8 to 6.1 meters or more above the ground, and their flight seems tireless. Some aeshnids feed at twilight above the treetops. Many of the smaller damselflies fly only 25 to 50 mm above the surface of the water. Some species of Anisoptera make long, even transoceanic, dispersal flights (see Corbet 1999).

Most dragonflies feed on a variety of insects that they catch on the wing in a basketlike arrangement of the legs or with their mouthparts. Dragonflies may eat their prey on the wing or may alight to devour it. The prey is chiefly small flying insects such as midges, mosquitoes, and small moths, but larger dragonflies often capture bees, butterflies, or other dragonflies. Odonata normally take moving prey, but some damselflies glean stationary prey from perches. If captured, dragonflies will eat or chew on almost anything that is put into their mouth—even their own abdomen!

Pond species are frequently found with numbers of small, globular, usually reddish bodies attached to the underside of the thorax or abdomen. These are the larvae of water mites. The mite larvae attach to the odonate nymph in the water and, when the nymph emerges to transform to the adult stage, the mite larvae move onto the adult. The mites spend one to three weeks on the dragonfly adults, feeding on their hemolymph and growing larger. Sometime during the odonate host's return to water, the mite larvae drop off and eventually complete their complex life cycle by developing into free-living, predaceous adults. It is not unusual to find dragonflies with dozens of mite larvae on them. Parasitic mites do not appear to do a great deal of damage to Odonata.

Classification of the Odonata

A synopsis of the nearly 450 species of Odonata occurring in North America north of Mexico is given next, with synonyms and alternate spellings in parentheses. The numbers in parentheses following each family are the numbers of North American species, taken mainly from Westfall and May (1996) and Needham, Westfall, and May (2000).

- Suborder Anisoptera—dragonflies
  - Superfamily Aeshnoidea
    - Petaluridae (2)—petaltails, graybacks
    - Gomphidae (97)—clubtails
    - Aeshnidae (Aeschnidae) (39)—darners
  - Superfamily Cordulegastroidea
    - Cordulegastridae (Cordulegasteridae) (8)—spiketails, biddies
  - Superfamily Libelluloidea
    - Corduliidae (58)—cruisers, emeralds, green-eyed skimmers
    - Libellulidae (114)—skimmers
- Suborder Zygoptera—damselflies
  - Calopterygidae (Agrionidae, Agriidae) (8)—broad-winged damselflies
  - Lestidae (18)—spreadwinged damselflies
  - Protoneuridae (Coenagrionidae in part) (3)—threadtails
  - Coenagrionidae (Coenagriidae, Agrionidae) (99)—pond damsels, narrow-winged damselflies
  - Platystictidae (1)—shadow damsels

The separation of the families of Odonata is based primarily on characters of the wings and head. We use the Comstock-Needham system of wing vein nomenclature. This includes a number of special terms not used in other orders and is illustrated in Figures 10–5 and 10–6. Riek and Kukalová-Peck (1984) proposed a reinterpretation of dragonfly wing venation on the basis of fossil specimens. A comparison between their scheme and that used here is presented in Table 10–1. The separation of genera and species is based on wing venation, color pattern, structure of the genitalia, and other characters. Useful recent guides to identifying the genera and species of North American Odonata are Westfall and May (1996) for Zygoptera and Needham, Westfall

Table 10–1 Comparison of Interpretations of Dragonfly Venation

Comstock-Needham	Riek and Kukalová-Peck (1984)
C	Costal margin (PC + CA + CP + ScA)
Sc	ScP
R + M basally	Paired or fused stems of RA and RP
R_1	RA
Rs	Radial supplement
M_{1+2}	RP1–2
M_1	RP1
M_2	RP2
M_3	RP3–4
M_4	MA
Cu basally	MP
Cu_1	MP
Cu_2	CuA
1A	CuP
Anal crossing	CuP crossing

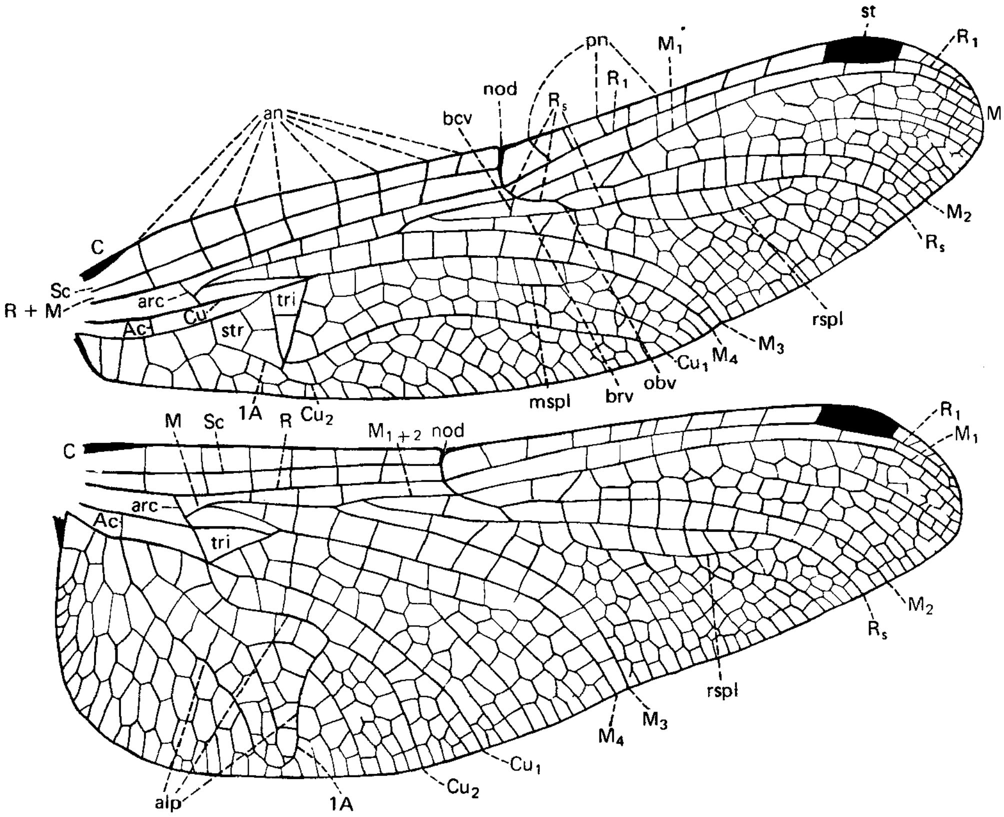


Figure 10–5 Wings of *Sympetrum rubicundulum* (Say) (Libellulidae), showing the Comstock-Needham system of terminology. *Ac*, anal crossing (A branching posteriorly from Cu; often called the cubitoanal crossvein); *alp*, anal loop (foot-shaped in this species); *an*, antenodal crossveins; *arc*, arculus (the upper part is M, and the lower part is a crossvein); *bcv*, bridge cross vein; *brv*, bridge vein; *mspl*, medial supplement; *nod*, nodus; *obv*, oblique vein; *pn*, postnodal crossveins; *rspl*, radial supplement; *st*, stigma; *str*, subtriangle (3-celled in this wing); *tri*, triangle (2-celled in front wing, 1-celled in hind wing). The usual symbols are used for the other venational characters.

and May (2000) for Anisoptera. Many species of Odonata can be recognized in the field without capture by using binoculars to view their characteristic size, shape, color, or habits (Dunkle 2000). Because of their popularity, the Dragonfly Society of the Americas has devised and standardized a list of English vernacular names for all species known to occur in North America (www.ups.edu/biology/museum/NAdragons.html).

Key to the Families of Odonata

This key deals only with adults. A key to the nymphs of Odonata may be found in Westfall (1987).

1. Front and hind wings similar in shape, narrow at base (Figures 10–6, 10–7D,F,G); wings at rest held either together above body or slightly divergent; compound eyes separated by a distance greater than width of 1 eye; males with 4 appendages at end of abdomen (Figure 10–4C,D) (damselflies, suborder Zygoptera) 2

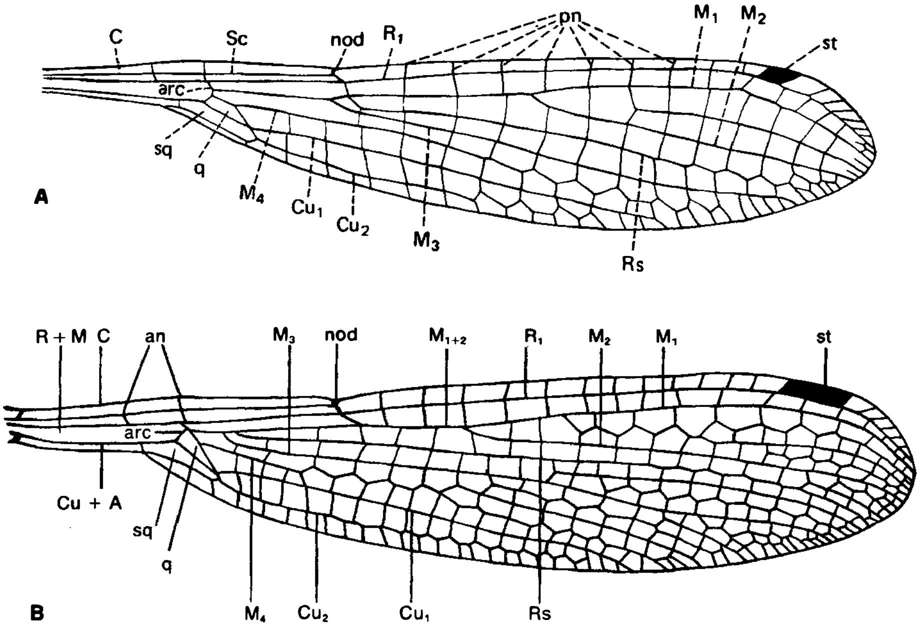


Figure 10–6 Hind wings of damselflies. A, *Enallagma* (Coenagrionidae); B, *Lestes* (Lestidae). *q*, quadrangle; *sq*, subquadrangle.

1′.	Hind wings wider than front wings, particularly at base (Figures 10–5, 10–7A–C); wings at rest held horizontally or nearly so; compound eyes contiguous or separated by a distance less than width of eye; males with 3 appendages at end of abdomen (Figure 10–4A) (dragonflies, suborder Anisoptera)	6	
2(1).	Ten or more antenodal crossveins (Figure 10–7D); wings not stalked, often with black, brown, or red markings; quadrangle with several crossveins	Calopterygidae	p. 205
2′.	Two antenodal crossveins (Figures 10–6 and 10–7F); wings stalked at base, either hyaline or lightly tinged with brown (rarely black); quadrangle without crossveins	3	
3(2′).	M_3 and Rs arising nearer arculus than nodus (Figure 10–6B); wings usually held divergent at rest	Lestidae	p. 205
3′.	M_3 and Rs arising nearer nodus than arculus (Figure 10–6A), usually arising below nodus; wings usually held together at rest	4	
4(3′).	Anal vein and Cu_2 long, reaching level of nodus; quadrangle distinctly trapezoidal (Figure 10–6A)	Coenagrionidae	p. 205
4′.	Anal vein and Cu_2 absent or reduced to length of 1 cell; quadrangle roughly rectangular (Figure 10–7F)	5	
5(4′).	Crossvein present in cubitoanal space proximal to anal crossing (Figure 10–7F); Cu_1 at least 10 cells in length	Platystictidae	p. 205
5′.	No crossvein in cubitoanal space proximal to anal crossing (Figure 10–7G); Cu_1 at most 3 cells in length	Protoneuridae	p. 205
6(1′).	Triangles in front and hind wings similar in shape, about equidistant from arculus (Figure 10–7A); most costal and subcostal crossveins not in line; usually a brace vein (an oblique crossvein; Figure 10–7E, bvn) present behind proximal end of pterostigma	7	

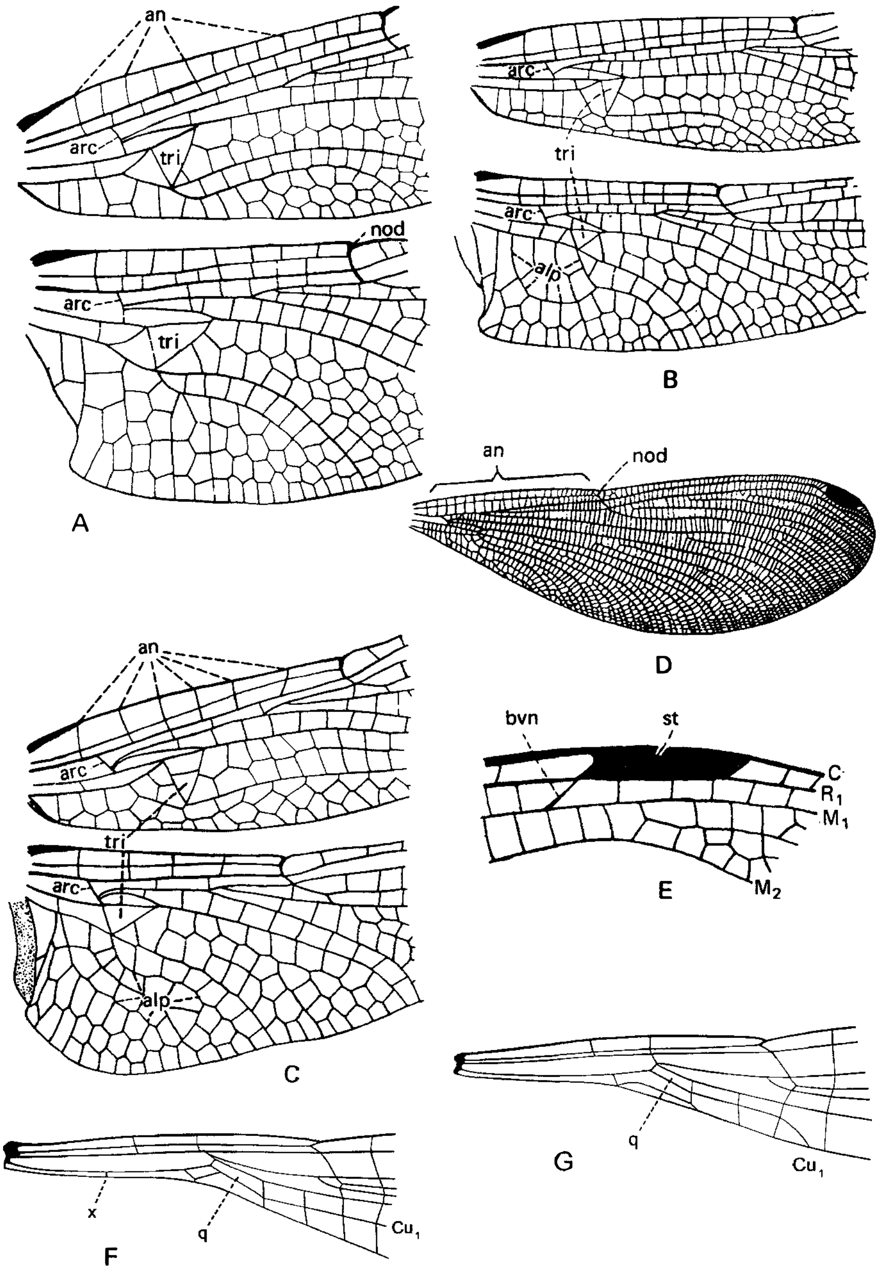


Figure 10–7 Wings of Odonata. A, Base of wings of *Gomphus* (Gomphidae); B, Base of wings of *Didymops* (Corduliidae); C, Base of wings of *Epitheca* (Corduliidae); D, Front wing of *Calopteryx* (Calopterygidae); E, Stigmal area of wing of *Aeshna* (Aeshnidae); F, Base of front wing of *Palaemnema domina* Calvert (Platystictidae); G, Base of front wing of *Neoneura aaroni* Calvert (Protoneuridae). *alp*, anal loop; *an*, antenodal crossveins; *arc*, arculus; *bvn*, brace vein; *nod*, nodus; *q*, quadrangle; *st*, stigma; *tri*, triangle; *x*, crossvein in cubitoanal space.

6′.	Triangles in front and hind wings usually not similar in shape, triangle in front wing farther distad of arculus than triangle in hind wing (Figure 10–5, 10–7B,C); most costal and subcostal crossveins in line; no brace vein behind proximal end of pterostigma	10	
7(6).	No brace vein behind proximal end of pterostigma; eyes barely meeting or slightly separated dorsally; if meeting, contiguous by less than width of lateral ocellus	Cordulegastridae	p. 203
7′.	Brace vein present behind proximal end of pterostigma (Figure 10–7E, bvn); eyes either broadly contiguous by more than width of lateral ocellus or widely separated	8	
8(7).	Compound eyes contiguous on dorsum of head for a distance greater than width of lateral ocellus (Figure 10–8B)	Aeshnidae	p. 203
8′.	Compound eyes separated on dorsum of head by distance greater than width of lateral ocellus (Figure 10–8A)	9	
9(8′).	Median lobe of labium notched (Figure 10–9A); pterostigma at least 8 mm in length	Petaluridae	p. 202

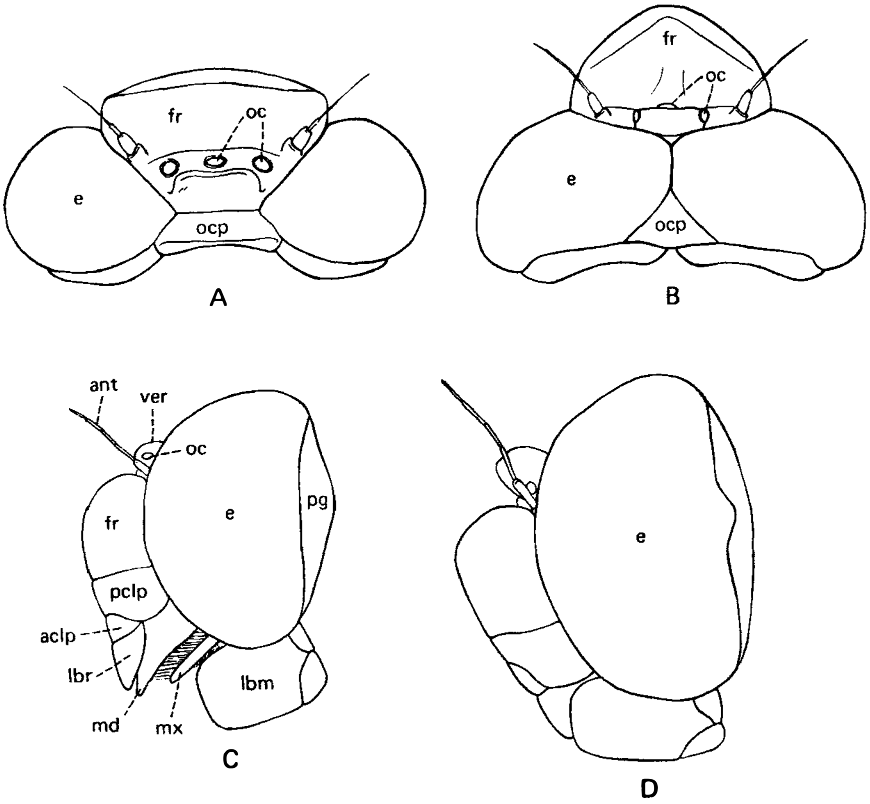


Figure 10–8 Head structure in dragonflies. A, *Gomphus exilis* Selys (Gomphidae), dorsal view; B, *Basiaeschna janata* (Say) (Aeshnidae), dorsal view; C, *Sympetrum* (Libellulidae), lateral view; D, *Epitheca* (Corduliidae), lateral view. *aclp*, anteclypeus; *ant*, antenna; *e*, compound eye; *fr*, frons; *lbm*, labium; *lbr*, labrum; *md*, mandible; *mx*, maxilla; *oc*, ocellus; *ocp*, occiput; *pclp*, postclypeus; *pg*, postgena; *ver*, vertex.

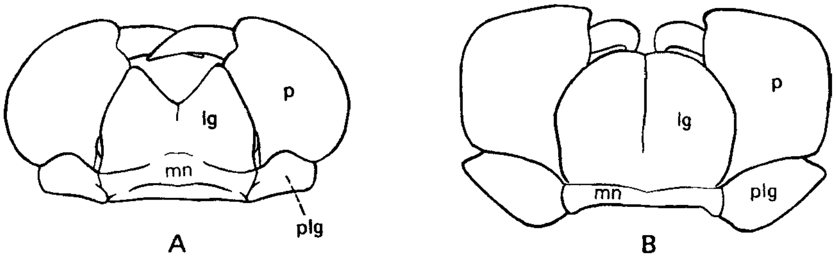


Figure 10–9 Labia of adult dragonflies. A, *Tachopteryx* (Petaluridae); B, *Aeshna* (Aeshnidae). *lg*, ligula or median lobe; *mn*, mentum; *p*, palp or lateral lobe; *plg*, palpiger or squama.

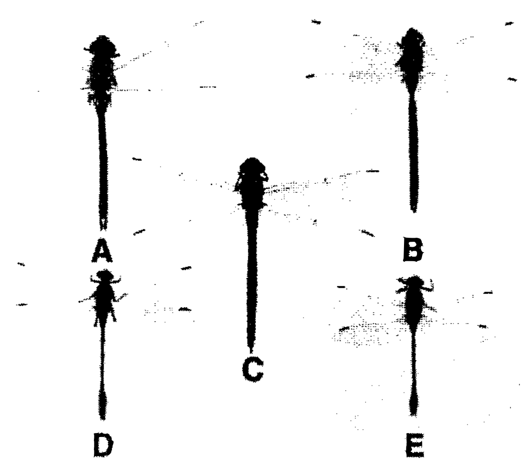
9′.	Median lobe of labium not notched (Figure 10–9B); pterostigma less than 8 mm in length	Gomphidae	p. 202
10(6′).	Hind margin of compound eyes lobed (Figure 10–8D); males with small lobe on each side of second abdominal segment; inner margin of hind wing of male somewhat notched; anal loop rounded (Figure 10–7B) or elongate, if foot-shaped with little development of "toe" (Figure 10–7C)	Corduliidae	p. 203
10′.	Hind margin of compound eyes straight (Figure 10–8C); males without small lobe on side of second abdominal segment; inner margin of hind wing of male not notched; anal loop with inner margin of "toe" usually well developed (Figure 10–5)	Libellulidae	p. 203

Suborder Anisoptera—Dragonflies

Dragonflies have hind wings that are wider at the base than the front wings, and the wings are held horizontal (or nearly so) at rest. The hind wings of the male in all but the Libellulidae are somewhat notched at the anal angle (Figure 10–7A–C), whereas the hind wings of all Libellulidae and the females of the other families have a rounded anal angle (Figure 10–5). The head is somewhat rounded to slightly transversely elongate, and in dorsal view is not wider than the thorax. The males have three appendages at the apex of the abdomen, two cerci (the superior appendages) and the epiproct (the inferior appendage), which may be bifid. The females of some groups have a well-developed ovipositor, whereas others either have a poorly developed ovipositor or entirely lack one. The nymphs have five short, stiff appendages at the apex of the abdomen and have epithelial gills in the rectum.

Family **Petaluridae—Petaltails, Graybacks:** Two species in this family occur in North America: *Tachopteryx thoreyi* (Hagen), the gray petaltail, in the eastern United States and *Tanypteryx hageni* (Selys), the black petaltail, in the Northwest (California and Nevada to southern British Columbia). Adults of *T. thoreyi* are grayish brown and about 75 mm in length. They usually occur along small streams in wooded valleys, where they often alight on tree trunks. Nymphs hide under dead leaves in seepage areas. Adults of *T. hageni* are smaller, about 55 mm in length, and black with yellow markings. They are found typically at higher elevations. The nymphs of this species burrow in permanently wet soil under moss.

Family **Gomphidae—Clubtails:** This is a fairly large group, and most of its members live along streams or lake shores. The clubtails range from 30 to 90 mm in length and are usually dark with yellowish or greenish markings (Figure 10–10D,E). Almost all species have clear wings. Many have swollen terminal abdominal segments, hence the common name for the group. They generally alight on a bare flat surface, although



Dwight M. DeLong

Figure 10–10 Aeshnoidea. A, *Anax junius* (Drury), male (Aeshnidae); B, *Aeshna constricta* Say, male (Aeshnidae); C, *Cordulegaster obliquus* (Say), female (Cordulegastridae); D, *Dromogomphus spoliatus* (Hagen), male (Gomphidae); E, *Gomphus externus* Hagen, male (Gomphidae). About one third natural size.

many species perch on vegetation, and they are more secretive than most other dragonfly families. The larvae of most species bury themselves in soft or loose substrates of streams, ponds, or lakes. The largest genus in the family is *Gomphus*. The impressive, large dragonhunter, *Hagenius brevistylus* Selys, is black and yellow and often feeds on other dragonflies.

Family **Aeshnidae—Darners:** This group includes the largest and most powerful of the dragonflies. They range from 50 to 116 mm long, but most are about 65 to 85 mm. The common green darner, *Anax junius* (Drury), a common and widely distributed species that lives around ponds, has a greenish thorax, a bluish abdomen, and a targetlike mark on the upper part of the face (Figure 10–10A). The genus *Aeshna* includes a number of species, mosaic darners, most of which are to be found near marshes in the latter part of the summer. They are dark with blue or greenish markings on the thorax and abdomen (Figure 10–10B). One of the largest species in this family is *Epiaeschna heros* (Fabricius), the swamp darner, an early summer species about 85 mm in length and dark brown with indistinct greenish markings on the thorax and abdomen.

Family **Cordulegastridae—Spiketails, Biddies:** The spiketails are large brown or black dragonflies with yellow markings (Figure 10–10C). They differ from the Aeshnoidea in lacking a brace vein at the proximal end of the pterostigma. These dragonflies are usually found along small, clear, woodland streams. The adults fly slowly up and down the stream, 0.3 to 0.7 m above the water, but if disturbed can fly very rapidly. The group is a small one, and all species in the United States belong to the genus *Cordulegaster*.

Family **Corduliidae—Cruisers, Emeralds, Green-Eyed Skimmers:** These dragonflies are mostly black or metallic green, although some are brown. Their conspicuous light markings are usually yellow. In life, the eyes of many species are brilliant green. The flight is usually direct, in many species interrupted by periods of hovering. Most members of this group are more common in Canada and the U.S. North than in the South.

Cruisers (Macromiinae, formerly Macromiidae) can be distinguished from emeralds by the rounded anal loop that lacks a bisector (Figure 10–7B). Two genera occur in the United States, *Didymops* and *Macromia*. The brown cruisers (*Didymops*) are light brown with light yellow markings on the thorax and abdomen. They live along streams and pond or lake shores. The river cruisers (*Macromia*) are large species that occur along lake shores and large streams. These dragonflies are dark brown to shiny, blackish green with yellow stripes on the thorax and yellow markings on the abdomen (Figure 10–11C,D). The eyes of living *Macromia* are usually brilliant green. *Macromia* are extremely fast fliers.

The emeralds (Corduliinae) are more diverse than the cruisers. The genus *Epitheca* (baskettails) contains brown to blackish dragonflies, usually 32–48 mm in length, often with brownish color at the base of the hind wing. They occur chiefly around ponds and swamps. The prince baskettail, *Epitheca princeps* (Hagen), is the only corduliid in North America with large brown spots at the tip of the wing. It is about 75 mm in length, with three blackish spots in each wing: basal, nodal, and apical. It lives around ponds. The largest genus in this group is *Somatochlora*, or striped emeralds. Most species in this group are metallic in color and more than 50 mm in length, and they usually occur along small, wooded streams or in bogs.

Family **Libellulidae—Skimmers:** Most species in this group live around ponds and swamps, and many are quite common. These dragonflies vary in length from about 20 to 75 mm, and many species have wings marked with spots or bands. The flight is usually rather erratic. This is a large group, and only a few of the more common genera and species are mentioned here.

The smallest libellulid in the United States is the elfin skimmer, *Nannothemis bella* (Uhler), only 18–20 mm long. It occurs in bogs in the eastern states. The males are bluish with clear wings (Figure 10–12G), and the females are patterned with black and yellow and the basal third or more of the wings is yellowish brown. In *Nannothemis*, the anal loop of the hind wing is open-

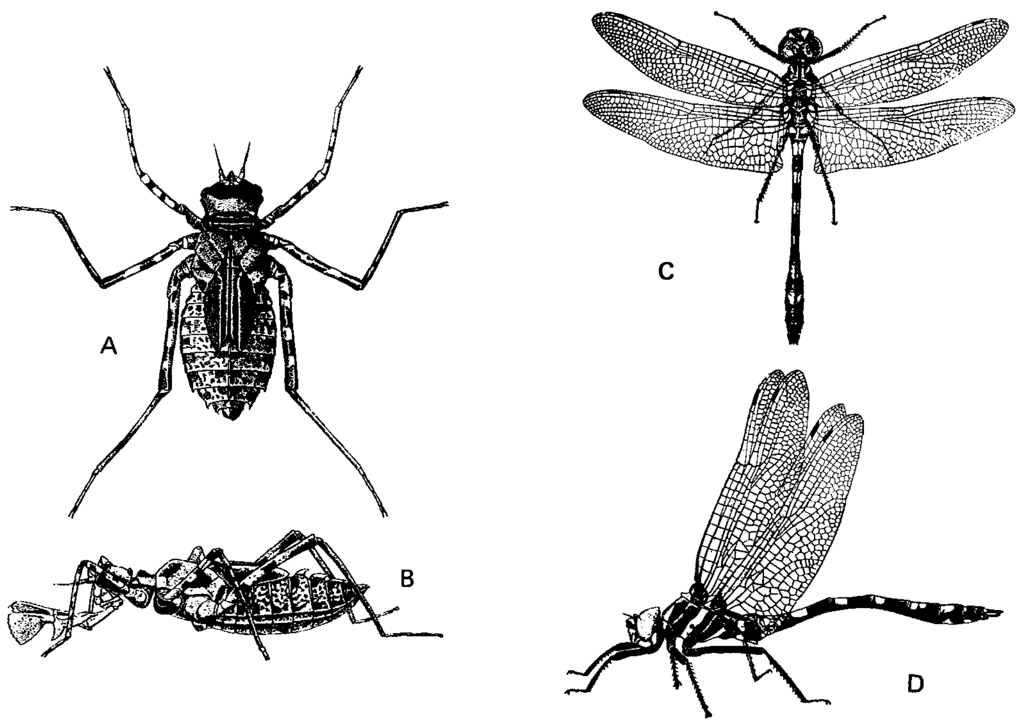
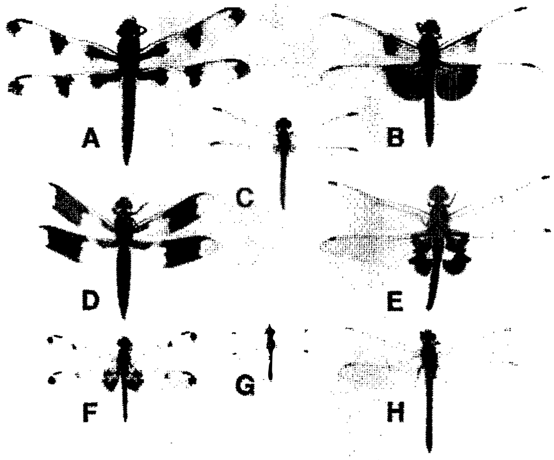


Figure 10–11 *Macromia magnifica* MacLachlan (Corduliidae). A, Nymph, dorsal view; B, Nymph, lateral view, with labium extended; C, Adult male, dorsal view; D, Same, lateral view. (Courtesy of Kennedy and the U.S. National Museum.)



Dwight M. DeLong

Figure 10–12 Libellulidae. A, *Libellula pulchella* Drury, male; B, *Libellula luctuosa* Burmeister, male; C, *Pachydiplax longipennis* (Burmeister), male; D, *Plathemis lydia* (Drury), male; E, *Tramea lacerata* Hagen, male; F, *Celithemis elisa* (Hagen), male; G, *Nannothemis bella* (Uhler), male; H, *Erythemis simplicicollis* (Say). About one third natural size.

ended, an exception in this family to the usual closed anal loop (Figure 10–5).

The large dragonflies that are common around ponds and have black spots or black and white spots on the wings are mostly species in the genus *Libellula*. The 12-spotted skimmer, *L. pulchella* Drury (Figure 10–12A), with a wingspread of about 90 mm, has three black spots (basal, nodal, and apical) on each wing, and the males have white spots between the black spots. The widow skimmer, *L. luctuosa* Burmeister, which is slightly smaller, has the basal third or so of each wing blackish brown, and the males have a white band beyond the basal dark coloring of the wing (Figure 10–12B).

The common whitetail, *Plathemis lydia* (Drury), has a wingspread of about 65 mm. The male has a broad, dark band across the middle of each wing, and the dorsal side of the abdomen is nearly white (Figure 10–12D). The females have spotted wings as in the females of *L. pulchella* and do not have a white abdomen. Pennants (*Celithemis*) are medium-sized (wingspread of about 50 mm), mostly reddish or brownish with darker markings, and with reddish or brownish spots on the wings (Figure 10–12F).

The eastern amberwing, *Perithemis tenera* (Say), with a wingspread of about 40 mm, has the wings amber-colored in the male and clear with brownish spots in the female. The meadowhawks (*Sympetrum*) are medium-sized, late-summer, marsh-dwelling insects. Their color varies from yellowish brown to a bright red, and the wings are usually clear except for a small basal spot of yellowish brown. The whiteface skimmers (*Leucorrhinia*) have a wingspread of about 40 mm and are dark, with a conspicuous white face. The most common species in the East is *L. intacta* Hagen, the dot-tailed whiteface, which has a yellow spot on the dorsal side of the seventh abdominal segment.

The blue dasher, *Pachydiplax longipennis* (Burmeister), is a common pond species, particularly in the central and southern United States. It varies in color from a patterned brown and yellow to a uniform bluish, and the wings are often tinged with brownish (Figure 10–12C). It has a long cell just behind the pterostigma and has a wingspread of 50 to 65 mm. The eastern pondhawk, *Erythemis simplicicollis* (Say), is a little larger than *P. longipennis*. It has clear wings, and the body color varies from light green patterned with black in females and immature males, to a uniform light blue in mature males (Figure 10–12H). The skimmers in the genera *Pantala* (gliders) and *Tramea* (saddlebags) are medium-sized to large (wingspread 75–100 mm), wide-ranging dragonflies that have a very broad base of the hind wings. Those in *Pantala* are yellowish brown or gray with a light yellowish or brownish spot at the base of the hind wing. Those in *Tramea* are largely black or dark, reddish brown with a black or dark brown spot at the base of the hindwing (Figure 10–12E).

Suborder Zygoptera—Damselflies

Damselflies have front and hind wings that are similar in shape, both narrowed at the base. The wings of the two sexes are similar in shape and at rest are held either together above the body or slightly divergent. The head is transversely elongate and in dorsal view is usually wider than the thorax. The males have four appendages at the apex of the abdomen: a pair of cerci (the superior appendages) and a pair of paraprocts (the inferior appendages). The females have an ovipositor, which usually makes the end of the abdomen look somewhat swollen. The nymphs have three gills at the apex of the abdomen, which may be leaflike, triquetrous, or sacculate (Figure 10–1).

Family **Calopterygidae—Broad-winged damsels:** The members of this group are relatively large damselflies that have the base of the wings gradually narrowed, not stalked as in other families of Zygoptera. These insects occur along streams. Two genera occur in the United States, *Calopteryx* and *Hetaerina*. The common eastern species of *Calopteryx* is the ebony jewelwing, *C. maculata* (Beauvois). The wings of the male are black, and those of the female are dark gray with a white pterostigma. The body is metallic greenish black. The most common species of *Hetaerina* is the American ruby-spot, *H. americana* (Fabricius), which is reddish in color, with a red or reddish spot in the basal third or fourth of the wings.

The remaining four families of Zygoptera have wings that are stalked at the base with only two antenodal crossveins. Most of the species are between 25 and 50 mm long, and nearly all have clear wings.

Family **Lestidae—Spreadwings:** The members of this group live chiefly in swamps and edges of ponds and lakes, but the adults occasionally wander some distance from the water. When alighting, these damselflies hold the body vertically, or nearly so, and the wings are partly outspread. They usually alight on plant or grass stems. There are two species of *Archilestes* in North America, but most species in this region (16) belong to the genus *Lestes*.

Family **Platystictidae—Shadow damsels:** One species in this tropical group, *Palaemnema domina* Calvert, has been found in southern Arizona. It is a blue, black, and brown species, 37–43 mm in length, that prefers shaded edges of streams in dry country. *Palaemnema* perch horizontally with wings together, occasionally flicking their wings open, and they are usually very difficult to find in tangles of roots and other riparian vegetation.

Family **Protoneuridae—Threadtails:** Three species in this tropical group, *Neoneura aaroni* Calvert, *N. amelia* Calvert, and *Protoneura cara* Calvert, occur in southern Texas. The *Neoneura* species are red and black, whereas the *Protoneura* species is orange and black. They range from 29 to 37 mm in length. Threadtails fly low over swiftly flowing and pooled portions of medium-sized to large streams, usually ovipositing in tandem in very small floating pieces of wood.

Family **Coenagrionidae—Pond damsels:** This large family has many genera and species. They range in length from 20 to 50 mm. These damselflies occur in a variety of habitats, some chiefly along streams and others around ponds or swamps. Most are rather feeble fliers and, when alighting, usually hold the body horizontal and wings together over the body (except *Chromagrion*, which holds the wings slightly spread). The two sexes are differently colored in most species, the males more brightly colored than the females. Many of these damselflies are beautifully colored in various combinations of blue, purple, red, orange, yellow, or green contrasting with black markings.

The dancers (*Argia*, Figure 10–13) are chiefly stream species, easily recognized by the long, close-set spurs on the tibiae and stout body. The males of the variable dancer, *Argia fumipennis* (Burmeister), a common species along streams and pond shores, are a beautiful violet color. Their wing color varies from clear in the northern and western parts of its range, to

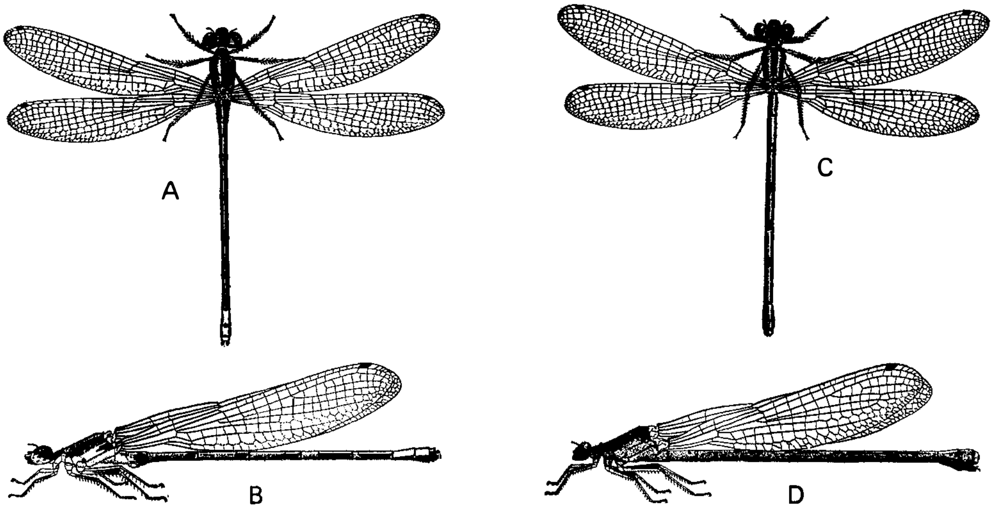


Figure 10–13 *Argia emma* Kennedy (Coenagrionidae). A and B, Male; C and D, Female. (Courtesy of Kennedy and the U.S. National Museum.)

brown or completely black in the Southeast. The sprites (*Nehalennia*), which also have fairly long tibial spurs, are small, slender, bronzy-green damselflies usually living in bogs and swamps. The eastern red damsel, *Amphiagrion saucium* (Burmeister), is a small, stout-bodied, red and black damselfly usually found in bogs.

The largest genus in this family in North America is *Enallagma*, called the **bluets**. Most species are light blue with black markings, although a few are predominantly orange or red. Several species of *Enallagma* may be found around the same pond or lake. Among the forktails (Figure 10–14), the eastern forktail, *Ischnura verticalis* (Say), is a very common species in the East (although uncommon further southeast) that occurs nearly wherever any damselfly is to be found. The males are mostly black, with narrow green stripes on the thorax and blue on the tip of the abdomen. Most females are bluish green with faint dark markings (older individuals) or brownish orange with black markings (recently emerged individuals). A very few females are colored like the males.

Collecting and Preserving Odonata

Many Odonata are powerful fliers, and capturing them on film or with a net is often a challenge. Some species are so adept on the wing that they can easily dodge a net, even when the net is swung like a baseball bat. Those who wish to catch, photograph, or observe with binoculars these fast-flying insects must study their flight habits. Many species have particular beats along which they fly at rather regular intervals or have perches on which they frequently alight. Someone familiar with the insect's habits can often anticipate where it will fly and be prepared for it. Swing at a flying dragonfly from behind. If approached from the

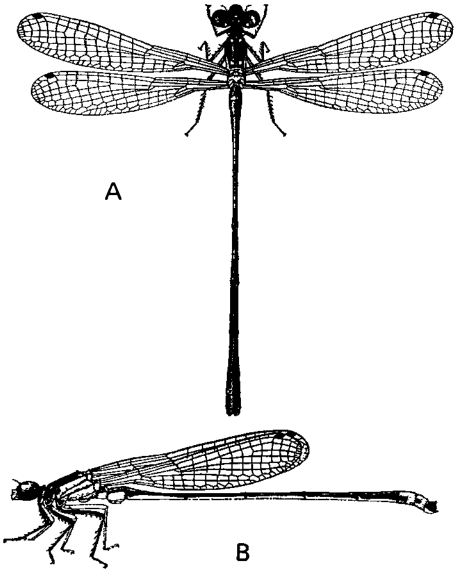


Figure 10–14 *Ischnura cervula* Selys, male (Coenagrionidae). A, Dorsal view; B, Lateral view. (Courtesy of Kennedy and the U.S. National Museum.)

front, the insect can see the net coming and can usually dodge it. In stalking a specimen, use only the slowest motions and try to approach from behind. Cover movements of your legs and feet by vegetation as much as possible, because dragonflies often see motion below them better than on a level with them.

The net used to capture Odonata should be an open-mesh net with little air resistance so it can be swung rapidly. The rim size and handle length depends on the collector, but for many species it is desirable to have a relatively large rim (300–380 mm in diameter) and a net handle at least 1 meter long.

Dragonflies beyond the reach of a net (many will fall in this category) can often be collected with a slingshot loaded with sand or with a gun loaded with dust shot. Many specimens so collected may be slightly damaged, but a slightly damaged specimen is usually better than none at all. For closeup photography, a macro lens is a necessity.

Odonata live in a great variety of habitats, and to observe a large number of species visit as many different habitats as possible. Two habitats that appear similar often contain different species, or the same habitat may harbor different species in different seasons. Many species have a short seasonal flight range, especially species whose flight period is restricted to the spring, and an observer must be in the field at just the right season to see them. Most species are found near aquatic habitats—ponds, streams, marshes, and the like—but many are wide-ranging and can be found in meadows, woodlands, and the hillsides above aquatic habitats. Emerging individuals can be found along stream and lake shores, either on flat surfaces or on the upright surfaces of rock and vegetation.

It is practically impossible to get close to many Odonata without wading, because they often fly at some distance from the shores of a pond or stream. Many species, particularly damselflies, can be obtained by sweeping in the vegetation along and near the shores of ponds and marshes. Others patrol along the edge of the emergent vegetation, where the water is a few feet deep. Stream species, which are usually rare in collections and are often locally distributed, are best collected by wading streams, if the streams are small enough. It is often necessary to wade for considerable distances.

Specimens collected for study should be placed alive in glassine or ordinary letter envelopes in the field, with the wings together above the body. Write locality data and collection date on the outside of the envelope. Record eye color of the living insects before placing them in the envelopes. If the specimens are to be put in a collection, keep them cool so they stay alive until time to preserve them.

The bright colors of Odonata generally fade quickly after the insect dies. Most color patterns can be retained if the specimens are killed in acetone and then left in acetone: 2 to 4 hours for Zygoptera and up to 24 hours for Anisoptera. It is best to put the specimens in glassine envelopes with the wings together. After soaking, immediately air-dry the specimens, preferably in an air-conditioned room or fume hood. The dried specimens are extremely brittle and should be handled very carefully. If one stores Odonata in any numbers, they are best kept in clear plastic envelopes or triangular paper envelopes (Figure 35–7), preferably one specimen to an envelope, never two species in the same envelope. For display, specimens may be pinned with the wings outspread, with the help of a spreading board, or, to save storage space, pin the specimen sideways, the pin passing through the thorax at the base of the wings and the left side of the insect uppermost.

The nymphs of Odonata may be collected by the various types of aquatic collecting equipment and methods described in Chapter 35. Zygoptera nymphs should be preserved directly in 70 to 75% ethanol. The anal gills are important structures in identifying damselfly nymphs to genus and species, but are easily dislodged from the abdomen. Therefore, it is best to put only a few individuals together in the same vial and not to put other insects in the vial with them. Nymphs of Anisoptera should be killed in boiling water, cooled to room temperature, and then immediately preserved in 75–80% ethanol. Preserve newly emerged odonate adults and their exuviae together, preferably in a vial of alcohol. Full-grown nymphs collected in the field can be brought back to the laboratory, preferably in wet moss, and reared in a fish-free, balanced aquarium. A stick or piece of screen must be provided for the nymphs to crawl out of the water, and the aquarium should be covered with a screen or cloth.

References

Bick, G. H. 1983. Odonata at risk in conterminous United States and Canada. Odonatologica 12:209–226.

Borror, D. J. 1945. A key to the New World genera of Libellulidae (Odonata). Ann. Entomol. Soc. Amer. 38:168–194; illus.

Bridges, C. A. 1994. Catalogue of the Family-Group, Genus-Group, and Species-Group Names of the Odonata of the World, 3rd ed. Champaign, IL: C. A. Bridges.

Byers, C. F. 1930. A contribution to the knowledge of Florida Odonata. Univ. Fla. Publ. Biol. Ser. No. 1, 327 pp.

Calvert, P. 1901–1909. Odonata. In Biologia Centrali Americana: Insecta Neuroptera, pp. 17–342, Suppl., pp. 324–420. London: Dulau.

Corbet, P. S. 1963. A Biology of Dragonflies. Chicago: Quadrangle, 247 pp.

Corbet, P. S. 1999. Dragonflies: Behavior and Ecology of Odonata. Ithaca, NY: Cornell University Press, 829 pp.

Dragonfly Society of the Americas. The Odonata of North America. http://www.ups.edu/biology/museum/NAdragons.html. Date accessed: November 20, 2003.

Dunkle, S. W. 2000. Dragonflies through Binoculars. A Field Guide to Dragonflies of North America. New York, NY. Oxford University Press, 266 pp.

Fraser, F. C. 1957. A Reclassification of the Order Odonata. Roy. Soc. Zool. New South Wales, Sydney. 133 pp.

Gloyd, L. K., and M. Wright. 1959. Odonata. In W. T. Edmondson (Ed.), Freshwater Biology, pp. 917–940. New York: Wiley.

Johnson, C. 1972. The damselflies (Zygoptera) of Texas. Bull. Fla. State Mus. Biol. Sci. 16(2):55–128.

Johnson, C., and M. J. Westfall, Jr. 1970. Diagnostic keys and notes on the damselflies (Zygoptera) of Florida. Bull. Fla. State Mus. Biol. Sci. 15(2):45–89.

Kennedy, C. H. 1915. Notes on the life history and ecology of the dragonflies of Washington and Oregon. Proc. U.S. Natl. Mus. 49:259–345.

Kennedy, C. H. 1917. Notes on the life history and ecology of the dragonflies of central California and Nevada. Proc. U.S. Natl. Mus. 52:483–635.

Montgomery, B. E. 1962. The classification and nomenclature of calopterygine dragonflies (Odonata: Calopterygoidea). Verh. XI. Int. Kongr. Ent. Wien 1960, 3(1962):281–284.

Musser, R. J. 1962. Dragonfly nymphs of Utah (Odonata: Anisoptera). Univ. Utah Biol. Ser. 12(6):1–66.

Needham, J. G., and E. Broughton. 1927. The venation of the Libellulidae. Trans. Amer. Entomol. Soc. 53:157–190.

Needham, J. G., and H. B. Heywood. 1929. A Handbook of the Dragonflies of North America. Springfield, IL.: C. C. Thomas, 378 pp.

Needham, J. G., and M. J. Westfall, Jr. 1955. A Manual of the Dragonflies of North America (Anisoptera). Los Angeles: University of California Press, 615 pp. (Reprinted 1975).

Needham, J. G., M. J. Westfall, Jr., and M. L. May. 2000. Dragonflies of North America, rev. ed. Gainesville, FL: Scientific Publ., 939 pp.

Paulson, D. R., and S. W. Dunkle. 1999. A checklist of North American Odonata. Tacoma, University of Puget Sound Occ. Pap. 56:1–86.

Pennak, R. W. 1978. Fresh-water invertebrates of the United States, 2nd ed. New York: Wiley Interscience, 803 pp.

Pritchard, G. 1986. The operation of the labium in larval dragonflies. Odonatologica 15:451–456.

Riek, E. F., and J. Kukalová-Peck. 1984. A new interpretation of dragonfly wing venation based upon early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. Can. J. Zool. 62:1150–1166; illus.

Ris, F. 1909–1919. Collections Zoologiques du Baron Edm. de Selys Longchamps. Bruxelles: Hayez, Impr. des Academies, Fasc. IX–XVI, Libellulinen 4–8, 1278 pp.

Robert, A. 1963. Libellules du Québec. Bull. 1, Serv. de la Faune, Ministère du Tourisme, de la Chasse et de la Pêche, Prov. Québec; 223 pp.

Smith, R. F., and A. E. Pritchard. 1956. Odonata. In R. L. Usinger (Ed.), Aquatic Insects of California. Berkeley: University of California Press, pp. 106–153.

Tillyard, R. J. 1917. The Biology of Dragonflies. Cambridge, UK: The University Press, 396 pp.

Waage, J. K. 1984. Sperm competition and the evolution of odonate mating systems. In R. L. Smith (Ed.), Sperm Competition and the Evolution of Animal Mating Systems, pp. 251–290. Academic Press, New York.

Walker, E. M. 1912. North American dragonflies of the genus *Aeshna*. Univ. Toronto Studies, Biol. Ser. No. 11, 214 pp.

Walker, E. M. 1925. The North American dragonflies of the genus *Somatochlora*. Univ. Toronto Studies, Biol. Ser. No. 26, 202 pp.

Walker, E. M. 1953. The Odonata of Canada and Alaska. Vol. 1: General, the Zygoptera—Damselflies. Toronto: University of Toronto Press, 292 pp.

Walker, E. M. 1958. The Odonata of Canada and Alaska, Vol. 2: The Anisoptera—Four Families. Toronto: University of Toronto Press, 318 pp.

Walker, E. M., and P. S. Corbet. 1975. The Odonata of Canada and Alaska, Vol. 3: The Anisoptera—Three Families. Toronto: University of Toronto Press, 307 pp.

Westfall, M. J., Jr. 1987. Order Odonata. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 95–177. Dubuque, IA: Kendall/Hunt, 754 pp.

Westfall, M. J., Jr., and M. L. May. 1996. Damselflies of North America. Gainesville, FL: Scientific Publishers, 649 pp.

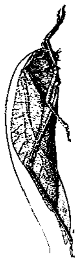
Westfall, M. J., Jr., and K. J. Tennessen. 1996. Odonata. In R. W. Merritt & K. W. Cummins (Eds.), An Introduction to the Aquatic Insects of North America, 3rd ed., pp. 164–211. Dubuque, IA: Kendall/Hunt.

Wright, M., and A. Peterson. 1944. A key to the genera of anisopterous dragonfly nymphs of the United States and Canada (Odonata, suborder Anisoptera). Ohio J. Sci. 44(4):151–166.

11

Order Orthoptera[1,2]

Grasshoppers, Crickets, and Katydids



The order Orthoptera contains a rather varied assemblage of insects, many of which are very common and well known. Most are plant feeders, and some of these are important pests of cultivated plants. A few are predaceous, a few are scavengers, and a few are more or less omnivorous.

The Orthoptera may be winged or wingless, and the winged forms usually have four wings. The front wings are usually elongate, many-veined, and somewhat thickened and are called *tegmina* (singular, *tegmen*). The hind wings are membranous, broad, and many-veined, and at rest they are usually folded fanwise beneath the front wings. Some species have one or both pairs of wings greatly reduced or absent. The body is elongate; the cerci are well developed (containing from one to many segments); and the antennae are relatively long (sometimes longer than the body) and have many segments. Many species have a long ovipositor, which is sometimes as long as the body. In others the ovipositor is short and more or less hidden. The tarsi usually have three to four segments. The mouthparts are of the chewing type (mandibulate), and metamorphosis is simple.

Sound Production in the Orthoptera

A great many types of insects "sing," but some of the best known insect singers (grasshoppers and crickets) are in the order Orthoptera. The songs of these insects are produced chiefly by stridulating, that is, by rubbing one body part against another (Figure 11–1). The singing Orthoptera usually have auditory organs—oval eardrums or tympana, located on the sides of the first abdominal segment (grasshoppers) or at the base of the front tibiae (katydids and crickets; Figure 11–4B, tym). These tympana are relatively insensitive to changes in pitch, but can respond to rapid and abrupt changes in intensity. The songs of grasshoppers, katydids, and crickets play an important role in their behavior, and the songs of different species are usually different. The significant differences are in rhythm.

The crickets (Gryllidae) and katydids (Tettigoniidae) produce their songs by rubbing a sharp edge (the scraper) at the base of the front wing along a filelike ridge (the file) on the ventral side of the other front wing (Figure 11–2 B–D). The bases of the front wings at rest lie one above the other. The left one is usually uppermost in the katydids, and the right is usually uppermost in the crickets. Both front wings have a file and a scraper, but the file is usually longer in the upper wing and the scraper is better developed in the lower wing. In the katydids, the lower (right) front wing usually contains more membranous area than the upper one. The file on the lower front wing and the scraper on the upper one are usually nonfunctional.

When the song is produced, the front wings are elevated (Figure 11–1) and moved back and forth; generally, only the closing stroke of the wings produces a sound. The sound produced by a single stroke of the front wings is called a *pulse*. Each pulse consists of a number of individual tooth strikes of the scraper on the file. The pulse rate in a given insect varies with the temperature, being faster at higher temperatures. In different species it varies from 4 or 5 per second to more than 200 per second.

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[1] Orthoptera: *ortho*, straight; *ptera*, wings.

[2] This chapter was edited by David A. Nickle and Thomas J. Walker.

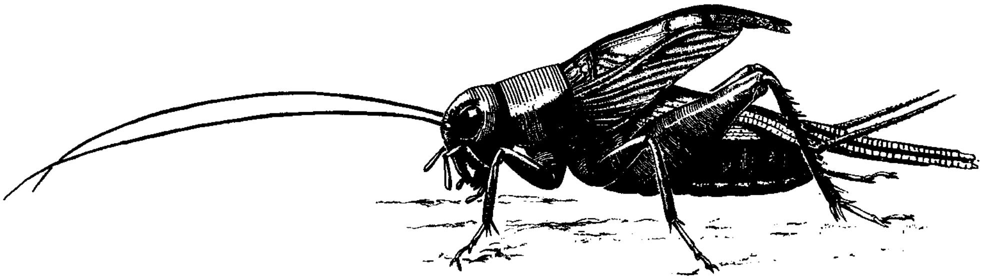

Figure 11–1 A field cricket singing (note elevated position of front wings). (Courtesy of R. D. Alexander.)

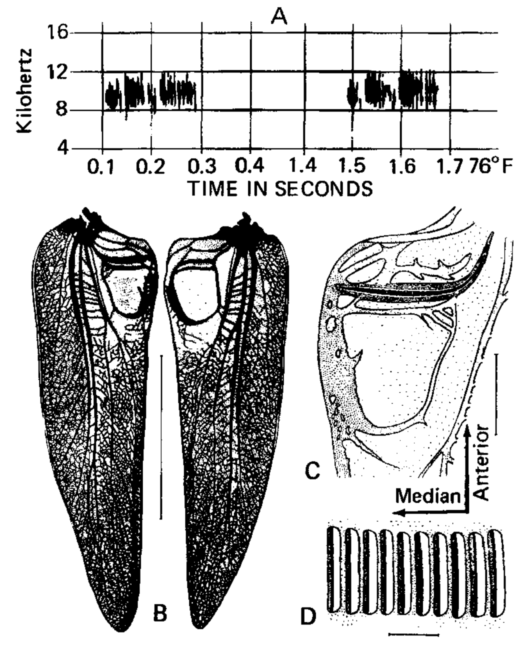

Figure 11–2 Song and sound-producing structures of the big green pine-tree katydid, *Hubbellia marginifera* (Walker) (Tettigoniidae, Tettigoniinae). A, audiospectrograph of two pulses of the song (4 kHz is approximately the pitch of the top note of the piano); B, front wings, dorsal view (line = 10 mm); C, ventral surface of basal portion of left front wing showing the file (line = 1 mm); D, several teeth of the file (line = 0.1 mm). (Courtesy of R. D. Alexander).

The songs of different species differ in the character of the pulses, in the pulse rate, and in the way the pulses are grouped. The pulses of crickets (Figure 11–3) are relatively musical; that is, they can usually be assigned a definite pitch, which in different species may range from 1,500 to 10,000 Hz (hertz, or cycles per second). The pulses of katydids (Figure 11–13) are more noiselike; that is, they contain a wide band of frequencies and cannot be assigned a definite pitch. The principal frequencies in the songs of some Orthoptera are quite high, between 10,000 and 20,000 Hz, and may be nearly or quite inaudible to some people. The pulses may be delivered at a regular rate for a considerable period, producing a prolonged trill (Figure 11–3E,F) or buzz (Figure 11–13D). They may be delivered in short bursts, a second or less in length, separated by silent intervals of a second or more (some tree crickets). They may be delivered in short series of a few pulses each (Figure 11–3A,B,D), producing chirps. They may be delivered in regularly alternating series of fast and slow pulses (meadow katydids, Figure 11–13B). Or the pulse rhythm may be more complex.

The band-winged grasshoppers (Gomphocerinae and Oedipodinae) usually make their noises by snapping their hind wings in flight. The noises so produced are crackling or buzzing. The slant-faced grasshoppers (Acridinae) "sing" by rubbing the hind legs across the front wings, producing a soft, rasping sound. The hind femora of these insects usually have a series of short, peglike structures that function something like a file (Figure 11–4H, strp).

The females of a few Orthoptera may make a few soft noises, but males do most of the singing. Grasshoppers usually move about while singing. Crickets and katydids are usually stationary. In all U.S. bush katydids, however, males sing, females respond with an acoustic tick sound, and males then move toward the sound produced by the female. Many Orthoptera, particularly some of the crickets and katydids, can produce two or more different types of sounds (Figure 11–3A–C). Each type is produced in certain circumstances, and each produces a characteristic reaction by the other individuals. The loudest and most commonly heard sound is the "calling song" (Figure 11–3A,D–F), which serves primarily to attract the fe-

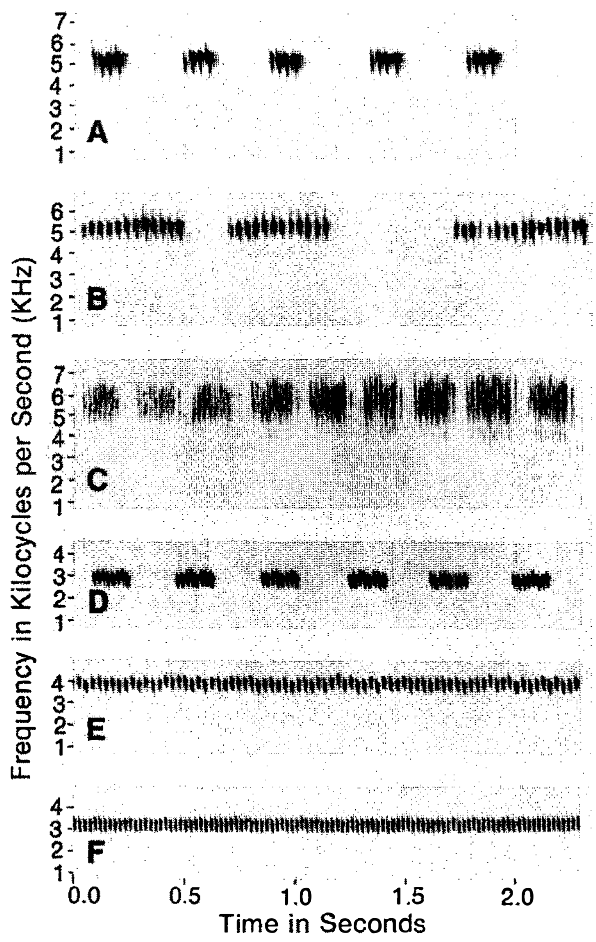

Figure 11–3 Audiospectrographs of cricket songs. A, calling song; B, aggressive song, and C, courtship song of a field cricket, *Gryllus pennsylvanicus* Burmeister; D, calling song of snowy tree cricket, *Oecanthus fultoni* Walker; E, calling song of the tree cricket, *Oecanthus argentinus* Saussure; F, calling song of the tree cricket, *Oecanthus latipennis* Riley. The pulse rate in E is 34 per second, and that in F is 44 per second.

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male. The female, if she is at the same temperature as the singing male, can recognize the song of her species and move toward the male. In the presence of another male, the males of some species produce an aggressive song (Figure 11–3B); this type of song is generally produced when a male's territory is invaded by another male. The field and ground crickets (Gryllinae and Nemobiinae) produce a special courtship song in the presence of a female (Figure 11–3C), which usually leads to copulation. A few Orthoptera (for example, the northern true katydid) produce "alarm" or "disturbance" sounds when disturbed or threatened with injury.

The majority of the singing Orthoptera sing only at night (Tettigoniidae and many Gryllidae); some sing only in the daytime (band-winged grasshoppers), and some sing both day and night (field, ground, and some tree crickets). Many species (for example, some of the cone-headed katydids and tree crickets) "chorus"; that is, when one starts to sing, other nearby individuals also begin to sing. In a few cases (for example, the snowy tree cricket), the individual pulses of the chorusing individuals may be synchronized, making it seem to a listener that only one insect is singing; in other cases the synchronization is less evident. In the case of the northern true katydid, a group whose songs are synchronized will alternate their songs with those of another such group, producing the pulsating "Katy did, Katy didn't" sound commonly heard on summer evenings in the East.

Classification of the Orthoptera

Until rather recently, this order of the Orthoptera included not only the grasshoppers, crickets, and katydids, but also the mantids (order Mantodea), walkingsticks (Phasmatodea), cockroaches (Blattodea), and rock crawlers (Grylloblattodea). Few entomologists will deny that these groups—along with the earwigs (Dermaptera), webspinners (Embiidina), and termites (Isoptera)—are relatively generalized Neoptera, and they are generally referred to as the orthopteroid orders. We have chosen to maintain a conservative approach to the classification of the orthopteroid orders, while admitting that many affinities pointed out by other authors (such as between termites, cockroaches, and mantids) certainly have merit and that many of the subfamilies we recognize may deserve family rank.

A synopsis of North American Orthoptera, as treated in this book, is given next. Other spellings, names, and arrangements are given in parentheses.

Classification of the Orthoptera

Suborder Caelifera
  Infraorder Acridomorpha
    Superfamily Eumastacoidea
      Eumastacidae (Acrididae in part)—monkey grasshoppers
    Superfamily Pneumoroidea
      Tanaoceridae (Eumastacidae in part)—desert long-horned grasshoppers

- Superfamily Acridoidea
  - Romaleidae—lubber grasshoppers
  - Acrididae (Locustidae)—grasshoppers
    - Cyrtacanthacridinae
    - Podisminae
    - Melanoplinae
    - Leptysminae
    - Oedipodinae
    - Acridinae
    - Gomphocerinae
- Infraorder Tetrigoidea
  - Tetrigidae—pygmy grasshoppers and pygmy locusts
- Infraorder Tridactyloidea
  - Tridactylidae (Gryllidae in part, Gryllotalpidae in part)—pygmy mole crickets

- Suborder Ensifera
  - Superfamily Gryllacridoidea
    - Stenopelmatidae—Jerusalem, sand, or stone crickets
    - Gryllacrididae (Tettigoniidae in part)—leaf-rolling grasshoppers
    - Rhaphidophoridae (Ceuthophilinae)—cave or camel crickets
    - Anostostomatidae—silk-spinning crickets
  - Superfamily Tettigonioidea
    - Tettigoniidae—katydids
      - Copiphorinae—cone-headed katydids
      - Phaneropterinae—bush katydids
      - Pseudophyllinae—true katydids
      - Listroscelinae
      - Conocephalinae—meadow katydids
      - Decticinae—shield-backed katydids
      - Saginae—matriarchal katydid
      - Meconematinae—drumming katydid
      - Tettigoniinae—big green pine-tree katydid
    - Prophalangopsidae (Haglidae)—hump-winged crickets
  - Superfamily Grylloidea
    - Gryllidae—crickets
      - Oecanthinae—tree crickets
      - Eneopterinae—bush crickets
      - Trigonidiinae—bush crickets
      - Nemobiinae—ground crickets
      - Gryllinae—house and field crickets
      - Brachytrupinae—short-tailed crickets
      - Pentacentrinae—anomalous crickets
  - Superfamily Gryllotalpoidea
    - Gryllotalpidae—mole crickets
  - Superfamily Mogoplistoidea
    - Mogoplistidae—scaly crickets
    - Myrmecophilidae—ant-loving crickets

Key to the Families of Orthoptera

Adults (and some nymphs) of North American Orthoptera may be identified to family by means of the following key. Families marked with an asterisk (*) are relatively rare and are unlikely to be taken by a general collector.

1.	Front legs much dilated and modified for digging (Figure 11–18); tarsi 3-segmented; length 20–35 mm	Gryllotalpidae	p. 219
1′.	Front legs not so enlarged, or if they are slightly enlarged (Tridactylidae) the front and middle tarsi are 2-segmented and the insect is less than 10 mm in length	2	
2(1′).	Front and middle tarsi 2-segmented, hind tarsi 1-segmented or absent; front legs somewhat dilated and fitted for digging; abdomen with apparently 2 pairs of stylelike cerci; 4–10 mm	Tridactylidae	p. 218
2′.	Tarsi 3- or 4-segmented, or if front and middle tarsi are 2-segmented (Tetrigidae), then hind tarsi are 3-segmented; front legs not dilated; abdomen with a single pair of cerci; length usually over 10 mm	3	
3(2′).	Hind tarsi 3-segmented, front and middle tarsi 2- or 3-segmented; ovipositor short; antennae usually short, seldom more than half as long as the body (Figures 11–6 through 11–9); auditory organs (tympana), if present, on sides of first abdominal segment	4	
3′.	Tarsi 3- or 4-segmented; ovipositor usually elongate; antennae long, usually as long as body or longer (Figures 11–1, 11–14 through 11–17); auditory organs, if present, at base of front tibiae (Figure 11–4B, tym)	8	

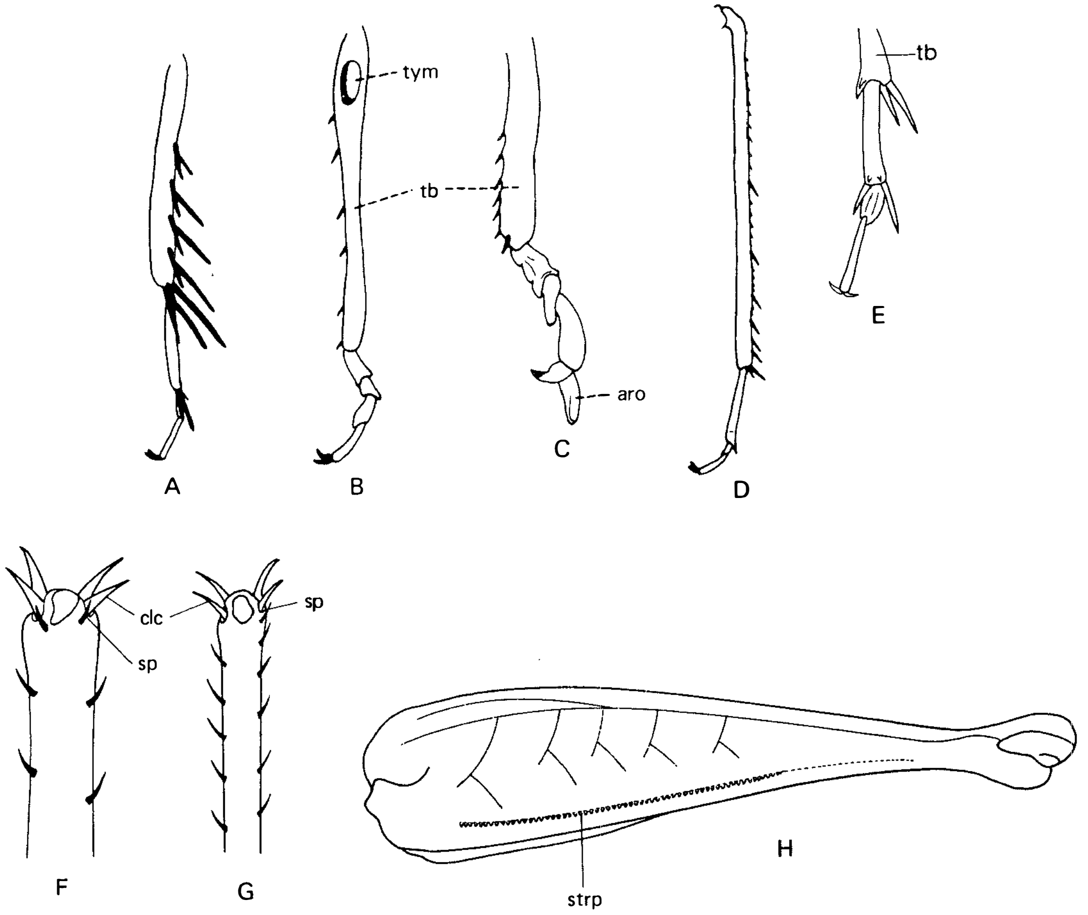

Figure 11–4 Leg structure in Orthoptera. A–E, tibiae and tarsi; F–G, apical portion of left hind femur; H, hind femur, mesal view. A, *Nemobius* (Nemobiinae, Gryllidae), hind leg; B, *Scudderia* (Phaneropterinae, Tettigoniidae), front leg; C, *Schistocerca* (Cyrtacanthacridinae, Acrididae); D, *Oecanthus* (Oecanthinae, Gryllidae), hind leg; E, *Phyllopalpus* (Trigonidiinae, Gryllidae), hind tarsus; F, *Romalea* (Romaleidae); G, *Melanoplus* (Melanoplinae, Acrididae); H, Acridinae (Acrididae). *aro*, arolium; *clc*, movable spines or calcaria; *cx*, coxa; *fm*, femur; *sp*, immovable spines; *stpr*, stridulatory pegs; *tb*, tibia; *ts*, tarsus; *tym*, tympanum.

4(3).	Pronotum prolonged backward over abdomen and tapering posteriorly (Figure 11–9); front wings vestigial; no arolia; front and middle tarsi 2-segmented, hind tarsi 3-segmented	Tetrigidae	p. 218
4′.	Pronotum not prolonged backward over abdomen (Figures 11–6 through 11–8); front wings usually well developed if hind wings are present; arolia present (Figure 11–4C); all tarsi 3-segmented	5	
5(4′).	Antennae shorter than front femora; wings absent; 8–25 mm in length; occurring in the chaparral country of the southwestern United States	Eumastacidae*	p. 215
5′.	Antennae longer than front femora; wings nearly always present; size variable, but usually over 15 mm in length; widely distributed	6	

6(5′).	Wings and tympana nearly always present; antennae not unusually long; males without a file on third abdominal tergum; widely distributed	7	
6′.	Wings and tympana absent; antennae very long, in males longer than body; males with a file on third abdominal tergum; southwestern United States	Tanaoceridae*	p. 215
7(6).	Hind tibia with both inner and outer immovable spines at apex (Figure 11–4F); prosternum usually with median spine or tubercle	Romaleidae	p. 215
7′.	Hind tibia with only the inner immovable spine at apex, outer one absent (Figure 11–4G); prosternum with or without median spine or tubercle	Acrididae	p. 215
8(3′).	All tarsi 3-segmented (Figure 11–4A,D,E); ocelli present or absent; ovipositor cylindrical or needle-shaped	9	
8′.	At least middle tarsi, and usually all tarsi, 4-segmented (Figures 11–4B, 11–10E); ocelli usually present; ovipositor sword-shaped	11	
9(8).	Wingless, broadly oval; hind femora much enlarged; eyes small and ocelli lacking; length 2–4 mm; living in ant nests	Myrmecophilidae	p. 225
9′.	Without the preceding combination of characters	10	
10(9′).	Wings very short or absent; hind tibiae without long spines (but with apical spurs); body covered with scales; hind femora stout; southern United States	Mogoplistidae	p. 225
10′.	Wings usually well developed; hind tibiae nearly always with long spines (Figure 11–4A); body not covered with scales; hind femora only moderately enlarged; widely distributed	Gryllidae	p. 223
11(8′).	Wings usually absent, but if present, then with 8 or more principal longitudinal veins; males lacking stridulatory structures on front wings; front tibiae with or without tympana; color usually gray or brown	12	
11′.	Wings present (but sometimes very small) and with fewer than 8 principal longitudinal veins; males with stridulatory structures on front wings (Figure 11–2 B–D); front tibiae with tympana; color variable, but often green	15	
12(11).	Antennae contiguous at base or nearly so	Rhaphidophoridae	p. 219
12′.	Antennae separated at base by a distance equal to or greater than length of first antennal segment	13	
13(12′).	Tarsi lobed, more or less flattened dorsoventrally; hind femora extending beyond apex of abdomen; eastern United States	Gryllacrididae	p. 219
13′.	Tarsi not lobed and more or less flattened laterally, hind femora not extending beyond apex of abdomen; western United States	14	
14(13′).	Base of abdomen and often head much wider than thorax; tibiae short and thick	Stenopelmatidae	p. 219
14′.	Base of abdomen and head almost the same width as thorax; tibiae thin	Anostostomatidae*	p. 219
15(11′).	Antennal sockets located about halfway between epistomal suture and top of head; wings reduced, broad in male, minute in female; ovipositor extremely short; hind femora extending to about apex of abdomen northwestern United States and southwestern Canada	Prophalangopsidae	p. 222
15′.	Antennal sockets located near top of head wings and ovipositor variable; hind femora usually extending beyond apex of abdomen	Tettigoniidae	p. 219

SUBORDER Caelifera: The Caelifera are jumping Orthoptera, with the hind femora more or less enlarged; they include the short-horned grasshoppers and the pygmy mole crickets. The antennae are nearly always relatively short, and the tarsi contain three or fewer segments. The tympana, if present, are located on the sides of the first abdominal segment. The species that stridulate usually do so by rubbing the hind femora over the tegmina or abdomen or snapping the wings in flight. All have short cerci and ovipositor.

***Family* Eumastacidae—Monkey Grasshoppers:** The members of this group live on bushes or trees in the chaparral country of the Southwest. They are wingless and remarkably agile. Their common name refers to their ability to progress through small trees and shrubs. Adults are slender, 8–25 mm in length, and usually brownish. The face is somewhat slanting; the vertex is pointed; and the antennae are very short (not reaching the rear edge of the pronotum). Monkey grasshoppers do not have a stridulatory organ on the sides of the third abdominal segment, as do the Tanaoceridae. This group is principally tropical, with 13 species in 3 genera occurring in the United States. They occur from central California, southern Nevada, and southwestern Utah south to southern California and southeastern Arizona.

***Family* Tanaoceridae—Desert Long-Horned Grasshoppers:** The members of this family resemble the monkey grasshoppers in being wingless and very active, and they occur in the deserts of the Southwest. They are grayish to blackish in color, relatively robust, and 8–25 mm in length. The face is less slanting than in the monkey grasshoppers, and the vertex is rounded. The antennae are long and slender, longer than the body in the male and shorter than the body in the female. Males have a stridulatory organ on the sides of the third abdominal segment. These grasshoppers are very seldom encountered. They are nocturnal and are likely to be found early in the season. Four species live in the United States (in the genera *Tanaocerus* and *Mohavacris*); they occur from southern Nevada to southern California.

***Family* Romaleidae—Lubber Grasshoppers:** These are robust, usually large grasshoppers (length mostly 25–75 mm) that are chiefly western in distribution. Some species have short wings and do not fly, and some have brightly colored hind wings. The only species in this group that normally occurs in the East is *Romalea microptera* (Beauvois), which occurs from North Carolina and Tennessee to Florida and Louisiana. This insect is 40–75 mm in length, with short wings, and the hind wings are red with a black border. This species is often used for morphological studies in beginning biology and entomology classes.

***Family* Acrididae—Grasshoppers:** This family includes most of the grasshoppers that are so common in meadows and along roadsides from midsummer until fall. The antennae are usually much shorter than the body, the auditory organs (tympana) lie on the sides of the first abdominal segment, the tarsi have three segments, and the ovipositor is short. Most are gray or brownish, and some have brightly colored hind wings. These insects eat plants and are often very destructive to vegetation. Most species pass the winter in the egg stage, the eggs being laid in the ground. A few overwinter as nymphs, and a very few overwinter as adults.

Many males in this group sing (during the day), either by rubbing the inner surface of the hind femur against the lower edge of the front wing or by snapping the hind wings in flight. Males in the former group (most slant-faced grasshoppers) have a row of tiny stridulatory pegs on the inner surface of the hind femur (Figure 11–4H, strp), and the sound produced is usually a low buzzing sound. In the latter group (band-winged grasshoppers), the song is a sort of crackling sound.

Key to the Subfamilies of Acrididae

There are differences of opinion regarding the number of subfamilies in this family. We follow Amadegnato (1974) and Otte (1995 a, b), who recognize Romaleidae as distinct from Acrididae and separate Acrididae into seven subfamilies in our fauna, which may be separated by the following key:

1.	Prosternum with median spine or tubercle (Figure 11–5A)	2	
1′.	Prostenum without median spine or tubercle	4	
2(1).	Usually very large species (40–65 mm long); mesosternal lobes usually longer than wide, inner margin of mesosternal lobe of mesosternum angulate (Figure 11–5E) (*Schistocerca*)	Cyrtacanthacridinae	p. 216
2′.	Smaller species (usually less than 40 mm long); mesosternal lobes wider than long, inner margin of mesosternal lobe of mesosternum rounded (Figure 11–5D)	3	

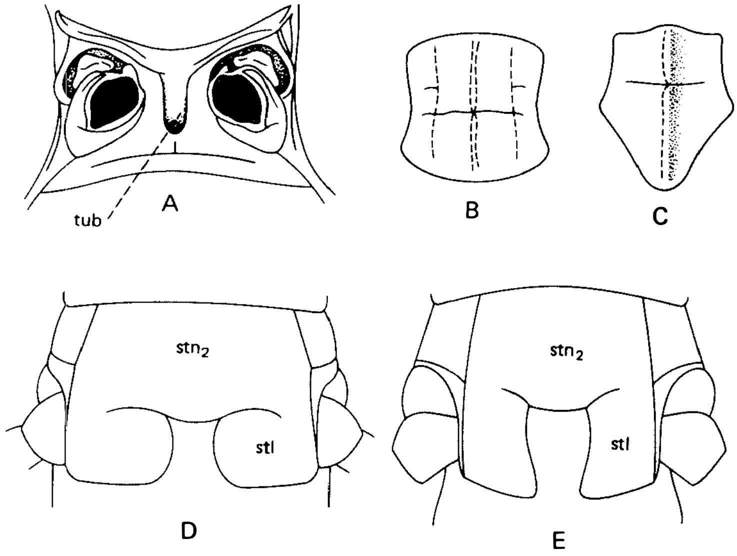

Figure 11–5 A, prothorax of *Melanoplus* (Melanoplinae, Acrididae), ventral view; B, pronotum of *Syrbula* (Acridinae, Acrididae), dorsal view; C, pronotum of *Chortophaga* (Oedipodinae, Acrididae), dorsal view; D, mesothorax of *Melanoplus* (Melanoplinae, Acrididae), ventral view; E, same, *Schistocerca* (Cyrtacanthacridinae, Acrididae). *stl*, mesosternal lobe; *stn*$_2$, mesosternum; *tub*, prosternal tubercle.

3(2′).	Elongated, slender species, with slanted faces and broad, flattened antennae; inner margins of mesosternal lobes touching; apex of hind wings usually pointed	Leptysminae	p. 217
3′.	Elongated or robust species, with rounded faces and thin, filiform antennae; inner margins of mesosternal lobes not touching; apex of hind wings usually rounded	Melanoplinae and Podisminae	p. 216
4(1′).	Face vertical or nearly so; antennae slender, filamentous, not flattened; pronotum usually with strong median ridge, caudal margin produced backward and mesally angulate (Figure 11–5C); wings long, reaching to or surpassing apex of abdomen; hind wings usually colored, often with black bands, separating areas that are clear or colored; hind femora of males without a row of stridulatory pegs; grasshoppers that often stridulate in flight	Oedipodinae	p. 217
4′.	Face usually slanting backward, sometimes strongly so; antennae either filiform or weakly flattened; pronotum flat, only rarely with a median ridge; caudal margin of pronotum truncate or rounded, not angulate mesally (Figure 11–5B); hind wing usually hyaline; wings variable in length, sometimes short and reaching apex of abdomen; grasshoppers that do not stridulate in flight, but usually with row of stridulatory pegs on hind femora of male (Figure 11–4H, strp), which are rubbed against the tegmina when the insect is at rest	Gomphocerinae and Acridinae	p. 217

Subfamily Cyrtacanthacridinae: The genus *Schistocerca* (Figure 11–6A) with 12 species is the only genus in this subfamily. Most of them are large and strong fliers. The desert locust, *S. gregaria* (Forkskål), of Africa, the "plague" species mentioned in the Bible, belongs to this group. It is one of the world's most destructive insects.

Subfamily Podisminae: These grasshoppers are very similar to the Melanoplinae. Twenty-three species are known from the United States.

Subfamily Melanoplinae: This is the largest subfamily of Acrididae with more than 300 species in 39 genera in the United States, most in the genus *Melanoplus*. Here belong our most common grasshoppers—and the

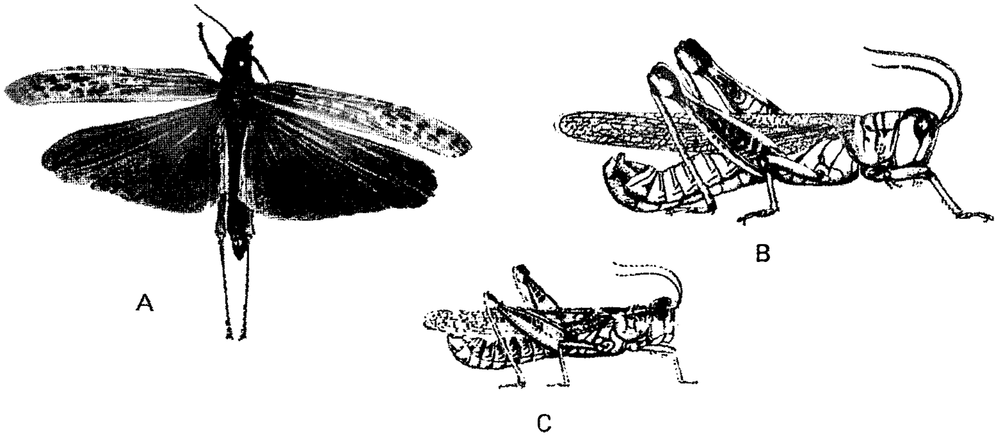

Figure 11–6 Spur-throated grasshoppers. A, *Schistocerca americana* (Drury), with wings outspread; B, *Melanoplus differentialis* (Thomas); C, *Melanoplus sanguinipes* (Fabricius). (A, courtesy of the Ohio Agricultural Research and Development Center; B–C, courtesy of USDA.)

ones that are most destructive. Most damage to U.S. crops by spur-throated grasshoppers is done by four species of *Melanoplus*: the migratory grasshopper, *M. sanguipes* (Fabricius) (Figure 11–6C); the differential grasshopper, *M. differentialis* (Thomas) (Figure 11–6B); the two-striped grasshopper, *M. bivittatus* (Say); and the red-legged grasshopper, *M. femurrubrum* (DeGeer).

Some species of spur-throated grasshoppers occasionally increase to tremendous numbers and migrate considerable distances, causing catastrophic damage. The migrating hordes of these insects may contain millions on millions of individuals and can literally darken the sky. From 1874 to 1877 great swarms of migratory grasshoppers appeared on the plains east of the Rocky Mountains and migrated to the Mississippi valley and to Texas, destroying crops whenever they stopped in their flight. This migratory behavior follows a tremendous buildup in numbers, resulting from a combination of favorable environmental conditions. When the numbers decrease, the insects do not migrate.

Subfamily Leptysminae: Most of these grasshoppers have a vertical face or nearly so, but a few, such as the slender grasshopper, *Leptysma marginicollis* (Serville), have a very slanting face and may be confused with some Gomphocerinae. There are only two species of this subfamily in the United States.

Subfamily Oedipodinae—Band-Winged Grasshoppers: These insects have brightly colored hind wings and generally frequent areas of sparse vegetation. They often alight on bare ground, with the hind wings concealed and the front wings blending with the background. These insects are quite conspicuous in flight, owing to the bright colors of the hind wings and the crackling sound sometimes made by the wings. The Oedipodinae are the only short-horned grasshoppers that stridulate while flying (the stridulation producing the crackling sound).

One of the more common species in this group is the Carolina grasshopper, *Dissosteira carolina* (L.), in which the hind wings are black with a pale border (Figure 11–7A). The clear-winged grasshopper, *Camnula pellucida* (Scudder), is an important pest species in this group. It has clear hind wings.

Subfamily Acridinae—Silent Slant-Faced Grasshoppers: Acridinae differ from Gomphocerinae in lacking stridulatory pegs on the inner face of the hind femur of the male. The only U.S. member of this subfamily is *Metaleptea brevicornis* (Johannson), found in the eastern states from southern Michigan and Wisconsin to Texas and Louisiana.

Subfamily Gomphocerinae—Stridulating Grasshoppers: The slanting face of these grasshoppers (Figure 11–8) distinguishes them from most other Acrididae, except the very slender grasshoppers in the Leptysminae. Males of most genera have a row of tiny stridulatory pegs on the inner surface of the hind femur (Figure 11–4H, strp). These pegs are lacking in the other subfamilies in North America. The Gomphocerinae usually lack a prosternal spine or tubercle, and the hind wings are usually hyaline.

The Gomphocerinae are not as abundant as the Melanoplinae and Oedipodinae and are most likely to be found along the borders of marshes, in wet meadows, and in similar places. They are rarely numerous enough to do much damage to vegetation.

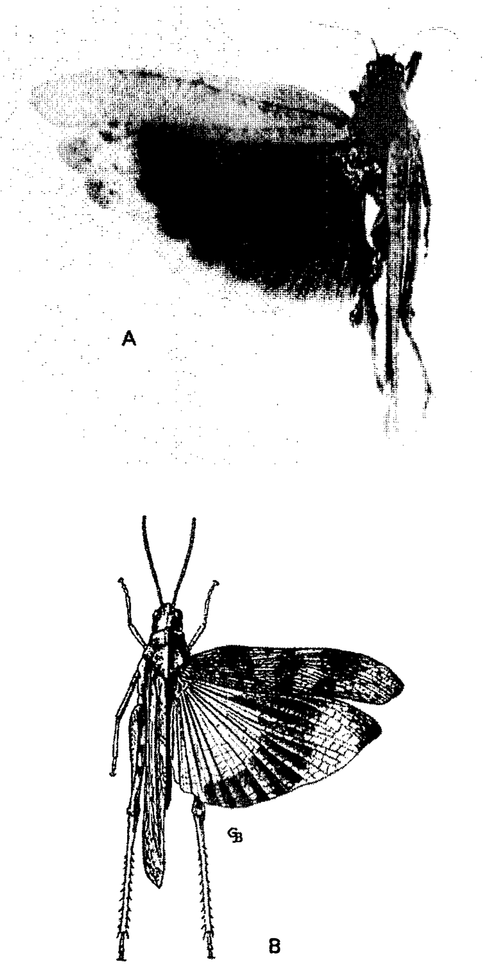

Figure 11–7 Band-winged grasshoppers. A, *Dissosteira carolina* (L.); B, *Spharagemon bolli* Scudder. (A, courtesy of Dwight M. Delong; B, courtesy of Institut de Biologie Générale, Université de Montréal.)

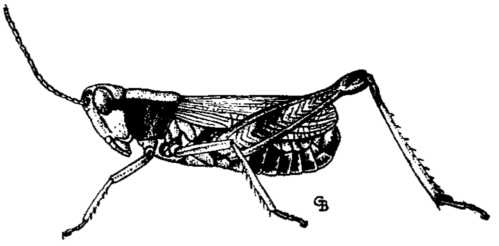

Figure 11–8 A slant-faced grasshopper, *Chloealtis conspersa* Harris. (Courtesy of Insititut de Biologie Générale, Université de Montréal.)

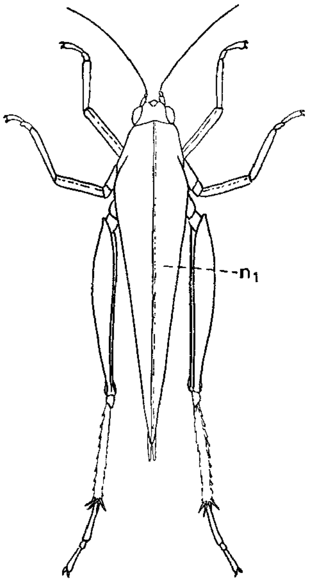

Figure 11–9 A pygmy grasshopper, *Tettigidea lateralis* (Say), $3\frac{1}{2}\times$. n_1, pronotum.

Family **Tetrigidae—Pygmy Grasshoppers or Grouse Locusts:** The pygmy grasshoppers may be recognized by the characteristic pronotum, which extends backward over the abdomen and is narrowed posteriorly (Figure 11–9). Most species are between 13 and 19 mm in length, and the females are usually larger and heavier bodied than the males. These are among the few grasshoppers that winter as adults. The adults are most often encountered in the spring and early summer. The pygmy grasshoppers are not of very much economic importance. In North America there are 27 species in six genera.

Family **Tridactylidae—Pygmy Mole Crickets:** These tiny crickets (length 4–10 mm) are burrowing in habit and usually occur along the shores of streams and lakes. They are very active jumpers, and when one is approached, it may seem to disappear suddenly. The tridactylids are peculiar among the Orthoptera in having what appear to be two pairs of cerci: four slender, stylelike appendages at the apex of the abdomen. These insects have no tympanal organs, and the males do not sing. Five species occur in North America, but they are widely distributed.

SUBORDER Ensifera: The Ensifera are jumping Orthoptera, with the hind femora more or less enlarged. They include the katydids and crickets. The antennae are nearly always long and hairlike, and the tarsi have three- or four -segments. The tympana, if present, are located on the upper ends of the front tibiae (Figure 11–4B). The species that stridulate do so by rubbing the edge of one front wing over a filelike ridge on the ventral side of the other front wing. Nearly all have a relatively long ovipositor, either sword-shaped or cylindrical.

Family **Stenopelmatidae—Jerusalem, Sand, or Stone Crickets:** These insects are 20–50 mm long, and the head and abdomen are rather large and robust. They are usually brownish, with black bands on the abdomen. They are generally found under stones or in loose soil. Four species of *Stenopelmatus* and five species of *Cnemotettix* represent this family in North America. They occur in the West and are most common in the Pacific Coast states.

Family **Gryllacrididae—Leaf-Rolling Grasshoppers:** This group is represented in the United States by one species: *Camptonotus carolinensis* (Gerstaecker), which occurs in the East from New Jersey to Indiana and south to Florida and Mississippi. This insect is nocturnal and feeds chiefly on aphids. During the day it shelters in a leaf rolled up and tied with silk spun from its own mouth.

Family **Rhaphidophoridae—Cave or Camel Crickets:** These insects are brownish and rather humpbacked in appearance (Figure 11–10) and live in caves, in hollow trees, under logs and stones, and in other dark, moist places. The antennae are often very long. Most species in this group belong to the genus *Ceuthophilus*, with 89 species in the United States and Canada.

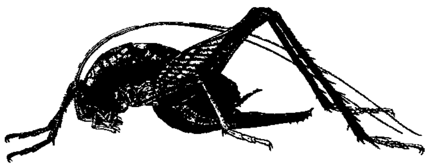

Figure 11–10 A cave cricket, *Ceuthophilus maculatus* (Harris), female. (Courtesy of Hebard and the Illinois Natural History Survey.)

Family **Anostostomatidae—Silk-Spinning Crickets:** The five species (four in the genus *Cnemotettix*) belonging to this family, spin silk from their maxillary glands. They are all found in the Channel Islands off the coast of California.

Family **Tettigoniidae—Katydids:** This is a large family, with 265 species in 50 genera in North America, whose members can usually be recognized by the long, hairlike antennae, the four-segmented tarsi, the auditory organs (when present) located at the base of the front tibiae, and the laterally flattened bladelike ovipositor. Most species have well-developed stridulating organs and are noted songsters. Each species has a characteristic song. The winter is usually passed in the egg stage, and in many species the eggs are inserted into plant tissues. Most species feed on plants, but a few prey on other insects.

Key to the Subfamilies of Tettigoniidae[2]

1.	Front wings oval and convex, costal field broad, with many parallel transverse veins; prosternal spine present; color green	Pseudophyllinae	p. 221
1′.	Front wings variable in shape, but costal field without transverse veins as described in the preceding entry; other characters variable	2	
2(1′).	Dorsal surface of first tarsal segment grooved laterally (Figure 11–11E); prosternal spines usually present (Figure 11–11D); front wings about as long as hind wings	3	
2′.	Dorsal surface of first tarsal segment smoothly rounded; prosternal spines absent; hind wings usually longer than front wings	Phaneropterinae	p. 220
3(2).	Anterior portion of vertex conical, sometimes acuminate, extending well beyond basal antennal segment (Figure 11–11C, ver)	Copiphorinae	p. 220
3′.	Anterior portion of vertex usually not conical or acuminate, not extending beyond basal antennal segment (Figure 11–11A,B, ver)	4	
4(3′).	Anterior portion of vertex laterally compressed, much less than half as wide as basal antennal segment (Figure 11–11A, ver); southwestern United States	Listroscelidinae	p. 221

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[2] The subfamilies Saginae and Meconematinae, each containing one species that has been introduced and established in the United States, are not included in this key. The subfamilies are discussed in the text.

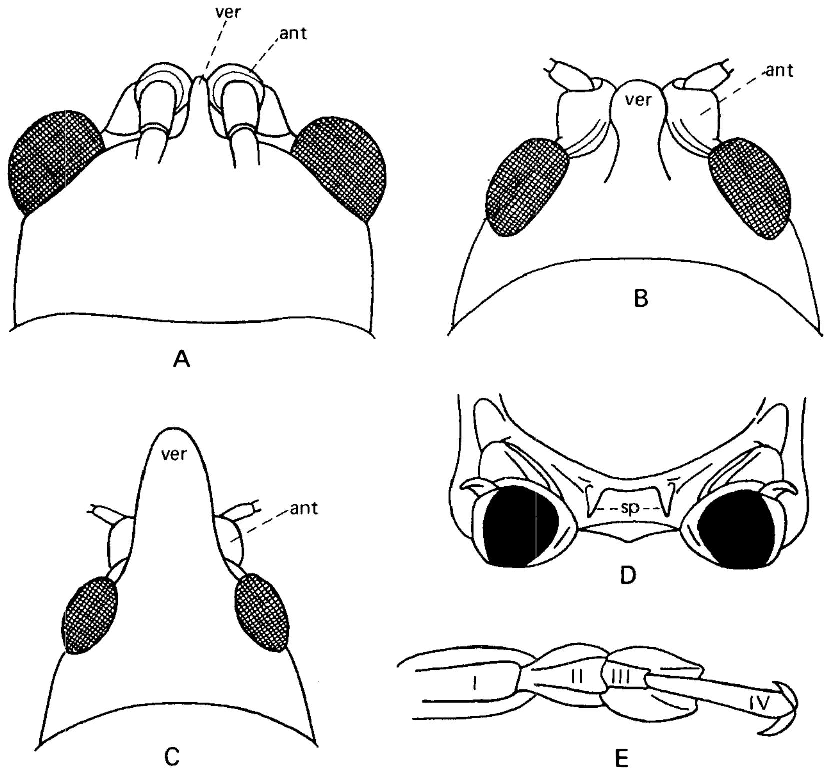


Figure 11–11 Characters of Tettigoniidae. A, head of *Rehnia* (Listroscelidinae), dorsal view; B, head of *Orchelimum* (Conocephalinae), dorsal view; C, head of *Neoconocephalus* (Copiphorinae), dorsal view; D, prothorax of *Orchelimum* (Conocephalinae), ventral view; E, hind tarsus of *Neoconocephalus* (Copiphorinae), dorsal view. *ant*, base of antenna; *sp*, prosternal spine; *ver*, vertex; *I–IV*, tarsal segments.

4′.	Anterior portion of vertex variable, but always more than half as wide as basal antennal segment; widely distributed	5	
5(4′).	One or more spines on dorsal surface of front tibiae	6	
5′.	No spines on dorsal surface of front tibiae	Conocephalinae	p. 221
6(5).	Pronotum extending back to abdomen (except in a few long-winged forms); wings usually greatly reduced; front wings usually gray, brown, or spotted; prosternal spines present or absent; widely distributed	Decticinae	p. 221
6′.	Pronotum never extending back to abdomen; wings always well developed; front wings green, rarely spotted with brown; prosternal spines present; southeastern United States	Tettigoniinae	p. 222

Subfamily **Copiphorinae—Cone-Headed Katydids:** The cone-heads are long-bodied katydids that have a conical head (Figure 11–12) and a long, swordlike ovipositor. They have two color phases, green and brown. They are generally found in high grass or weeds and are rather sluggish. Their jaws are very strong, and a person handling these insects carelessly may receive a healthy nip. This group is a small one, with only a few genera. The more common eastern species belong to the genus *Neoconocephalus*. The songs of cone-heads vary. In most cases the song is a prolonged buzz (Figure 11–13D), but in *N. ensiger* (Harris), a common eastern species, it is a rapid series of lisping notes (Figure 11–13C). These insects generally sing only at night.

Subfamily **Phaneropterinae—Bush Katydids:** The members of this and the next subfamily are well known for their songs, which are usually heard in the evening and at night. The katydids in this subfamily can be recognized by the absence of spines on the prosternum,

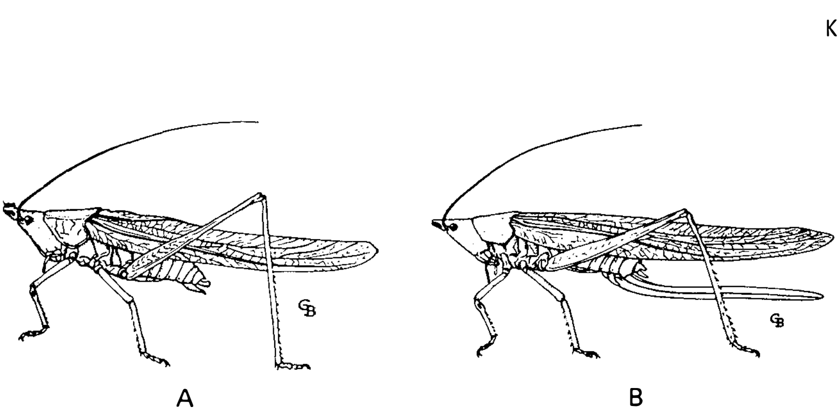
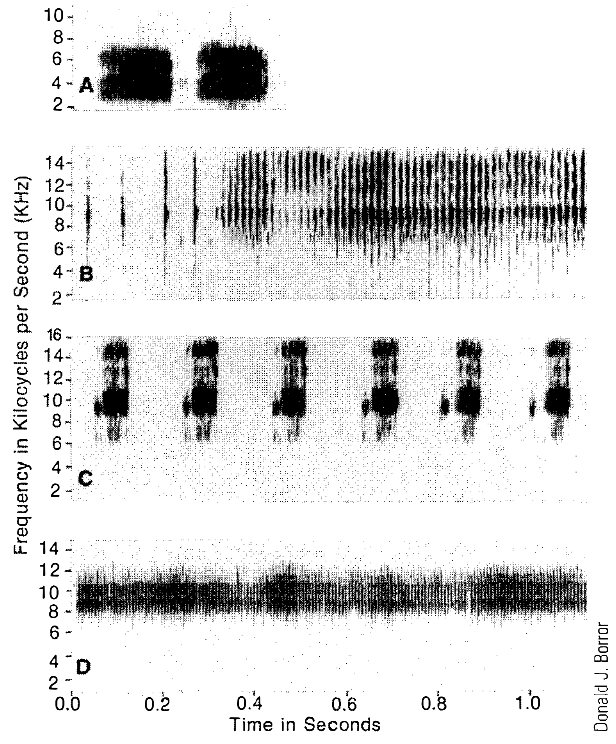


Figure 11–12 A cone-headed katydid, *Neoconocephalus ensiger* (Harris). A, male; B, female. (Courtesy of the Institut de Biologie Générale, Université de Montréal.)



Donald J. Borror

Figure 11–13 Audiospectrographs of the songs of katydids (Tettigoniidae). A, northern true katydid, *Pterophylla camellifolia* (Fabricus), a two-pulse song, the pulses uttered at the rate of about 5 per second; B, a meadow katydid, *Orchelimum nigripes* Scudder; C, a cone-headed katydid, *Neoconocephalus ensiger* (Harris), the pulses produced at the rate of about 5 per second; D, another cone-headed katydid, *N. nebrascensis* (Brunner), the pulses produced at the rate of about 146 per second. B, C, and D show only a part of the long-continued song of these insects.

and the hind wings are usually longer than the front wings; some western species are brachypterous. About 10 genera occur in the United States. The three most common genera in the East are *Scudderia* (bush katydids), *Microcentrum* (angular-winged katydids), and *Amblycorypha* (round-headed katydids). *Scudderia* has nearly parallel-sided front wings (Figure 11–14B,C); *Microcentrum* has somewhat angled front wings, with the hind femora not extending beyond the front wings (Figure 11–14A). *Ambylcorypha* has elongate-oval front wings, and the hind femora extend beyond the apex of the front wings. These katydids are normally green, but pink forms occasionally occur; these color forms are not distinct species.

Subfamily Pseudophyllinae—True Katydids: These katydids are principally arboreal in habit, living in the foliage of trees and shrubs. The northern true katydid, *Pterophylla camellifolia* (Fabricius), is the insect whose "Katy did, Katy didn't" song is heard so commonly on summer evenings in the Northeast. Its song contains from two to five pulses (Figure 11–13A). The southern representatives of this katydid sing a somewhat longer and faster song, containing up to about a dozen pulses.

Subfamily Listroscelidinae: These katydids are very similar to the Decticinae, and the U.S. genera (*Neobarrettia* and *Rehnia*) were formerly placed in that group. This subfamily is principally tropical in distribution and is represented in the United States by a few species in the south central states, from Texas north to Kansas.

Subfamily Conocephalinae—Meadow Katydids: These small to medium-sized, slender-bodied, usually greenish katydids (Figure 11–15) are found principally in wet, grassy meadows and along the margins of ponds and streams. Two genera are common in the eastern United States, *Orchelimum* (usually over 18 mm in length) and *Conocephalus* (usually less than 17 mm long).

Subfamily Decticinae—Shield-Backed Katydids: These insects are brownish to black, short-winged, and usually 25 mm or more in length. The pronotum extends back to the abdomen. Most species appear cricketlike. The eastern species, most of which belong to the genus *Atlanticus*, occur in the dry upland woods. The majority of the Decticinae occur in the West, where they may live in fields or woods. Some of the western species often do serious damage to field crops. The Mormon cricket, *Anabrus simplex* Haldeman, is a serious pest in the Great Plains states, and the coulee

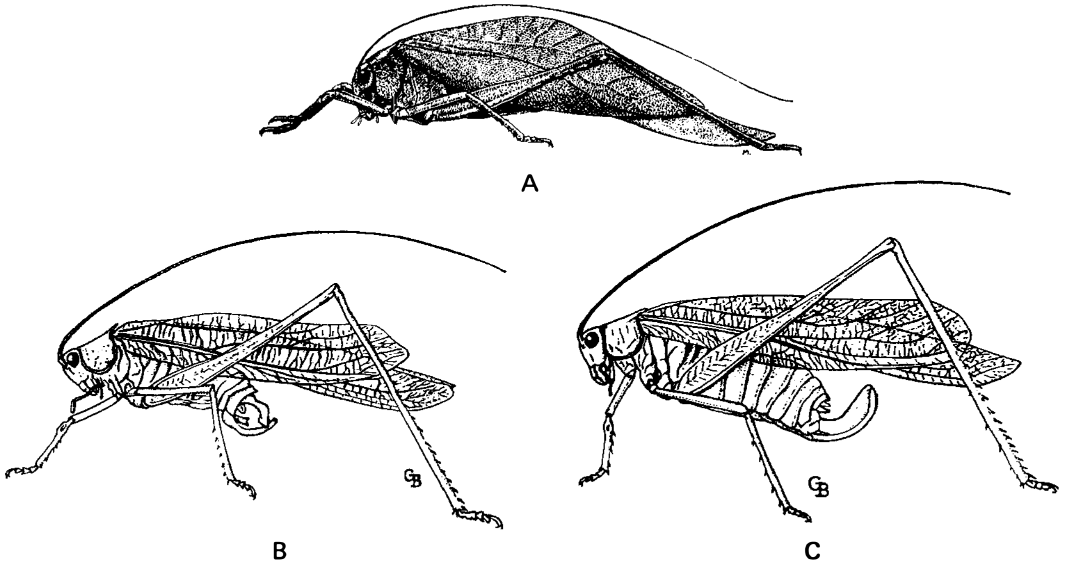


Figure 11–14 Bush Katydids. A, *Microcentrum rhombifolium* (Saussure); B, *Scudderia furcata* Brunner, male; C, *S. furcata* Brunner, female. (A, courtesy of Hebard and the Illinois Natural History Survey; B and C, courtesy of Institut de Biologie Générale, Université de Montréal.)

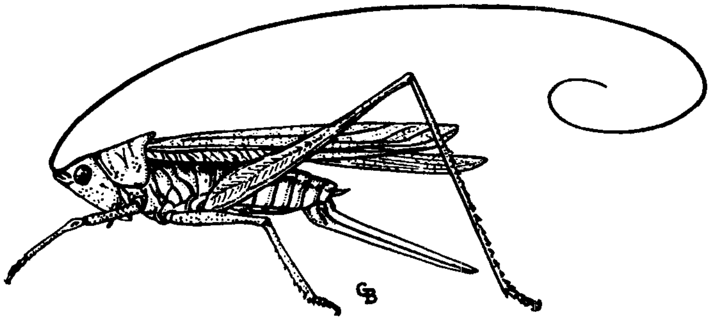


Figure 11–15 A meadow katydid, *Conocephalus fasciatus* (DeGeer), female. (Courtesy of the Institut de Biologie Générale, Université de Montréal.)

cricket, *Peranabrus scabricollis* (Thomas), often does considerable damage in the arid regions of the Pacific Northwest. The work of California gulls (*Larus californicus*) in checking an outbreak of the Mormon crickets in Utah in 1848 is now commemorated by a monument to the gull in Salt Lake City.

Subfamily Saginae: *Saga pedo* (Pallas), the matriarchal katydid, has been introduced from Europe and was established in Michigan. It has no potential for rapid spread and may even have died out. This insect has raptorial front and middle legs and is predaceous on other insects.

Subfamily Meconematinae: *Meconema thalassinum* (DeGeer), the drumming katydid, has been introduced from Europe is established in New York and Pennsylvania, and is rapidly spreading. It is a small, delicate, greenish insect with a rounded head, and the antennae are inserted between the eyes. This subfamily is well represented by some 200 species in the Palearctic region and Africa.

Subfamily Tettigoniinae: This group contains a single U.S. species, *Hubbellia marginifera* (Walker), the big green pine-tree katydid, which occurs in the southeastern United States. The song and song-producing structures of this katydid are illustrated in Figure 11–2.

***Family* Prophalangopsidae—Hump-Winged Crickets:** This family is represented in North America by two species of *Cyphoderris*, which occur in the mountains of the northwestern United States and southwestern Canada. Adults are brownish with light markings, relatively robust, and about 25 mm in length. In the Tettigoniidae, the left front wing is uppermost, and its file in the functional one. In this group either front wing may be uppermost, and the males may switch the position of the wings while singing. The song of *C. monstrosa* Uhler is a loud, very high-pitched (12–13 kHz) trill about 2 seconds in length or less, which has a slight pulsating quality apparently due to the switching of the front wings during the song.

***Family* Gryllidae—Crickets:** The crickets resemble the katydids in having long, tapering antennae; stridulating organs on the front wings of the male; and the auditory organs on the front tibiae, but differ from them in having not more than three tarsal segments, the ovipositor usually needlelike or cylindrical rather than flattened, and the front wings bent down rather sharply at the sides of the body. Many of these insects are well-known singers, and each species has a characteristic song. Most species overwinter as eggs, laid generally in the ground or vegetation. This family is represented in the United States by seven subfamilies, which can be separated by the following key.

Key to the Subfamilies of Gryllidae

1.	Second tarsal segment somewhat expanded laterally, flattened dorsoventrally (Figure 11–4E)	2	
1′.	Second tarsal segment small, flattened laterally (Figure 11–4A,D)	3	
2(1).	Hind tibiae with small teeth between longer spines; ovipositor cylindrical, usually straight; length 11–23 mm	Eneopterinae	p. 224
2′.	Hind tibiae without small teeth between longer spines; ovipositor compressed, upcurved; length 4.0–8.5 mm	Trigonidiinae	p. 224
3(1′).	Antennae inserted well below middle of face	Pentacentrinae	p. 225
3′.	Antennae inserted at or above middle of face	4	
4(3′).	Ocelli present; head short, vertical (Figures 11–1, 11–17); hind tibiae without teeth between spines (Figure 11–4A); black or brown insects	5	
4′.	Ocelli absent; head elongate, horizontal (Figure 11–16); hind tibiae usually with minute teeth between spines (Figure 11–4D); usually pale green insects	Oecanthinae	p. 223
5(4).	Spines of hind tibiae long and movable (Figure 11–4A); last segment of maxillary palps at least twice as long as preceding segment; body usually less than 12 mm long	Nemobiinae	p. 224
5′.	Spines of hind tibiae stout and immovable; last segment of maxillary palps only slightly longer than preceding segment; body usually over 14 mm in length	6	
6(5′).	Ocelli arranged in nearly a transverse row; ovipositor very short, often not visible; southeastern United States	Brachytrupinae	p. 225
6′.	Ocelli arranged in an obtuse triangle; ovipositor at least half as long as hind femora; widely distributed	Gryllinae	p. 224

Subfamily Oecanthinae—Tree Crickets: Most tree crickets are slender, whitish or pale green insects (Figure 11–16). All are excellent singers. Some species occur in trees and shrubs; others occur in weedy fields. The snowy tree cricket, *Oecanthus fultoni* Walker, a shrub inhabitant, chirps at a very regular rate, which varies with the temperature (Figure 11–3D). Adding 40 to the number of its chirps in 15 seconds gives a good approximation of the temperature in degrees Fahrenheit. Most species of tree crickets deliver loud trills. Some of the tree-inhabiting species have songs consisting of short bursts of pulses. Most North American tree crickets belong to the genus *Oecanthus*. The two-spotted tree cricket, *Neoxabea bipunctata* (DeGeer), differs from *Oecanthus* in lacking teeth on the hind tibiae, in having the hind wings much longer than the front

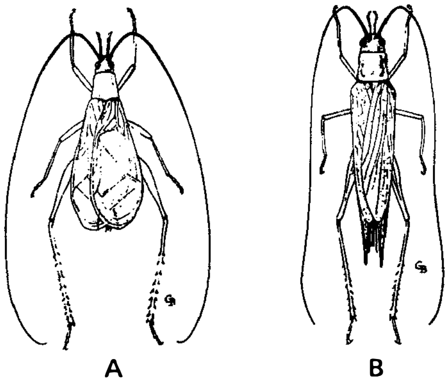


Figure 11–16 A tree cricket, *Oecanthus quadrimaculatus* Beutenmüller. A, male; B, female. (Courtesy of the Institut de Biologie Générale, Université de Montréal.)

wings, and in its buffy coloration. Tree crickets lay their eggs in bark or on stems (Figure 2–34 E) and often seriously damage twigs by their egg laying.

Subfamilies Eneopterinae and Trigonidiinae—Bush Crickets: The bush crickets are principally bush- or tree-inhabiting and are rarely found on the ground (where one would find the somewhat similar ground crickets). They differ from other crickets in having the second tarsal segment distinct and somewhat flattened and expanded laterally (Figure 11–4E). This segment is quite small and somewhat compressed in other crickets (Figure 11–4D). The Eneopterinae differ from the Trigonidiinae in being much larger (length 11–23 mm in the Eneopterinae and 4.0–8.5 mm in the Trigonidiinae) and in the shape of the ovipositor and the character of the spines on the hind tibiae (see key to subfamilies, couplet 2). Both groups are small and occur only in the eastern states.

The most common species in the Eneopterinae is the jumping bush cricket, *Orocharis saltator* Uhler, which is grayish brown in color and 14–16 mm in length. The two most common species in the Trigonidiinae are Say's bush cricket, *Anaxipha exigua* (Say), which is brownish and 6–8 mm in length, and the handsome or red-headed bush cricket, *Phyllopalpus pulchellus* Uhler, which is blackish, with the head and pronotum red, and 6–7 mm in length. The species of *Cyrtoxipha* (Trigonidiinae), which occur in the Southwest, are pale green in color.

Subfamily Nemobiinae—Ground Crickets: These crickets (Figure 11–17A) are common in pastures, in meadows, along roadsides, and in wooded areas. They are less than 13 mm in length and are usually brownish. The songs of most species are soft, high-pitched, and often pulsating trills or buzzes.

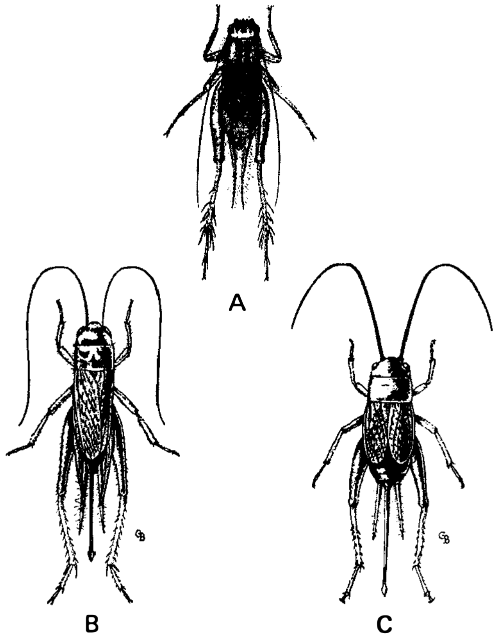


Figure 11–17 A, a ground cricket, *Allonemobius fasciatus* (DeGeer), male; B, the house cricket, *Acheta domesticus* (L.); C, a field cricket, *Gryllus pennsylvanicus* Burmeister. (A, courtesy of Hebard and the Illinois Natural History Survey; B and C, courtesy of the Institut de Biologie Générale, Université de Montréal.)

Subfamily Gryllinae—House and Field Crickets: These crickets are very similar to the ground crickets but are generally larger (more than 13 mm in length), and they vary from brownish to black. The field crickets (Figure 11–1) are very common in pastures, in meadows, along roadsides, and in yards, and some enter houses. The several species of *Gryllus* are very similar morphologically and were formerly considered to represent a single species. Now several species are recognized, which differ chiefly in habits, life history, and song. Most species of *Gryllus* chirp (Figure 11–3A), but one species occurring in the Southwest, *G. rubens* Scudder, produces a more or less long trill. The most common species of *Gryllus* in the East is probably the northern field cricket, *G. pennsylvanicus* Burmeister (Figure 11–17C). The house cricket, *Acheta domesticus* (L.), a species introduced into the United States from Europe, which often enters houses, differs from the native species of *Gryllus* in having a light-colored head with dark cross bars (Figure 11–17B). The members of this group sing both day and night. Other genera in this subfamily (*Miogryllus* and *Gryllodes*) occur in the southern states.

Subfamily Brachytrupinae—Short-Tailed Crickets: These crickets get their common name from the fact that their ovipositor is very short and often not visible, rather than long and slender as in most other crickets. The short-tailed crickets are burrowing in habit and usually occur in colonies, their burrows going 0.3 m or more into the ground. They spend most of the time during the day in their burrows and generally come out only at night. A single species of short-tailed cricket occurs in the southeastern states, *Anurogryllus muticus* (DeGeer). This insect is 12 to 17 mm long and yellowish brown.

Subfamily Pentacentrinae—Anomalous Crickets: This subfamily is represented in the United States by the single species *Trogonidimimus belfragei* Caudell in Oklahoma and northern Texas. The species may be collected at lights. This family is largely tropical in distribution.

***Family* Gryllotalpidae—Mole Crickets:** Mole crickets are brownish, very pubescent insects with short antennae, and the front legs are very broad and spadelike (Figure 11–18). These insects burrow in moist soil, usually near ponds and streams, often 150–200 mm below the surface. There is a tympanum on the front tibia, and the males sing. Only seven species of mole crickets occur in North America, six in the East and one in the West. The most common eastern species is *Neocurtilla hexadactyla* (Perty) (Figure 11–18). This insect is generally 25–30 mm in length, and its song is much like that of the snowy tree cricket (*Oecanthus fultoni* Walker) but is pitched lower. Mole crickets of the genus *Scapteriscus* often damage crops such as peanuts, tobacco, strawberries, and garden vegetables in the South Atlantic and Gulf Coast states.

Figure 11–18 The northern mole cricket, *Neocurtilla hexadactyla* (Perty). (Courtesy of Hebard and the Illinois Natural History Survey.)

***Family* Mogoplistidae—Scaly Crickets:** The members of this group are small, wingless or very short-winged, slender-bodied, flattened insects that are chiefly tropical in distribution. They occur on bushes or beneath debris in sandy localities near water. The body is covered with translucent scales that are easily rubbed off. The members of this group in the southern states are 5–13 mm in length.

***Family* Myrmecophilidae—Ant-Loving Crickets:** These crickets are small (2–4 mm in length) and broadly oval, with greatly dilated hind femora. They live in ant nests and feed (at least in part) on secretions from the ants. Of the half dozen or so North American species, only one, *Myrmecophila pergandei* Bruner, occurs in the East (from Maryland to Nebraska).

Collecting and Preserving Orthoptera

Many of the Orthoptera, because they are relatively large and numerous, are fairly easy to collect. The best time for collecting most species is from midsummer to late fall, although a few species should be looked for in early summer. The more conspicuous forms such as the grasshoppers and crickets, are most easily collected with a net, either by sweeping vegetation or by aiming for particular individuals. Some of the more secretive species can be collected at night by listening for their songs and then locating them with a flashlight, or by means of various sorts of baited traps. Some forms can be caught by putting molasses or a similar material in the bottom of a trap like that shown in Figure 35–6A. The insects so collected can simply be picked out of the trap.

Most nymphs and some soft-bodied adult specimens should be preserved in alcohol, but most adults can be pinned. Pin grasshoppers through the right side of the rear part of the pronotum or through the right tegmen. Pin crickets through the right tegmen, in about the middle (from front to rear) of the body. If the specimen is very soft-bodied, support the body by a piece of cardboard or by pins, or it will sag at either end. In the case of grasshoppers, spread the wings, at least on one side (as in Figure 11–8A), so the color and venation of the hind wing can be seen. It is sometimes desirable to eviscerate some of the larger grasshoppers before they are pinned, to facilitate drying and preservation. Make a short incision on the right or left side of the body near the base of the abdomen, and remove as much of the viscera as possible.

References

Alexander, R. D. 1957. The taxonomy of the field crickets of the eastern United States (Orthoptera, Gryllidae: *Acheta*). Ann. Entomol. Soc. Amer. 50:584–602.

Alexander, R. D., A. E. Pace, and D. Otte. 1972. The singing insects of Michigan. Great Lakes Entomol. 5:33–69.

Amedegnato, C. 1974. Les genres d'Acridiens neotropicaux, leur classification par familles, sous-familles et tribus. Acrida 3:193–204.

Bailey, W. J. and D. C. F. Rentz (eds.). 1990. The Tettigoniidae: biology, systematics and evolution. Berlin: Springer Verlag, 395pp.

Blatchley, W. S. 1920. Orthoptera of Northeastern America. Indianapolis: Nature, 785 pp.

Capinera, J. L., C. W. Scherer and J. M. Squitier. 2001. Grasshoppers of Florida. Gainsville: University Press Florida, 144 pp.

Chopard, L. 1938. La Biologie des Orthoptères. Paris: Lachevalier, 541 pp.

Dakin, M. E. J. and K. L. Hays. 1970. A synopsis of Orthoptera (sensu lato) of Alabama. Bull. Agric. Exp. Sta. Auburn University 404:1–118

Dirsch, V. M. 1975. Classification of the Acridomorphoid Insects. Oxford, UK: E. W. Classey, 178 pp.

Field, L. H. (ed.). 2001. The biology of wetas, king crickets and their allies. Wallingford, UK: CABI Publishing, 540 pp.

Froeschner, R. C. 1954. The grasshoppers and other Orthoptera of Iowa. Iowa State Coll. J. Sci. 29:163–354.

Gerhardt, H. C. and F. Huber. 2002. Acoustic communication in insects and anurans: common problems and diverse solutions. Chicago: University of Chicago Press, 531 pp.

Grant, H. J., Jr., and D. Rentz. 1967. Biosystematic review of the family Tanaoceridae, including a comparative study of the proventriculus (Orthoptera: Tanaoceridae). Pan-Pac. Entomol. 43:65–74.

Gwynne, D. T. 2001. Katydids and bush-crickets, reproductive behavior and evolution of the Tettigoniidae. Ithaca, NY: Cornell University Press, 317 pp.

Helfer, J. R. 1987. How to Know the Grasshoppers, Cockroaches, and Their Allies, 2nd ed. New York: Dover Publications, 363 pp.

Huber, F., T. E. Moore, and W. Loher (eds.). 1989. Cricket behavior and neurobiology. Ithaca, NY: Cornell University Press.

Jago, N. D. 1971. A revision of the Gomphocerinae of the world with a key to the genera (Orthoptera: Acrididae). Proc. Acad. Nat. Sci. Philadelphia 123(8):204–343.

Love, R. E., and T. J. Walker. 1979. Systematics and acoustic behavior of the scaly crickets (Orthoptera: Gryllidae: Mogoplistinae) of eastern United States. Trans. Amer. Entomol. Soc. 105:1–66.

Morris, G. K., and D. T. Gwynne. 1978. Geographical distribution and biological observations of *Cyphoderris* (Orthoptera: Haglidae) with a description of a new species. Psyche 85:147–166.

Nickle, D. A., T. J. Walker, and M. A. Brusven. 1987. Order Orthoptera. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 147–170. Dubuque, IA: Kendall/Hunt, 754 pp.

Otte, D. 1981. The North American Grasshoppers. Vol. 1: Acrididae, Gomphocerinae and Acridinae. Cambridge, MA: Harvard University Press, 275 pp.

Otte, D. 1984. The North American Grasshoppers. Vol. 2: Acrididae, Oedipodinae. Cambridge, MA: Harvard University Press, 366 pp.

Otte, D. 1994a. Orthoptera Species File, Number 1. Crickets (Grylloidea): A Systematic Catalog. Philadelphia: Philadelphia Academy of Sciences and The Orthoptera Society, 120 pp.

Otte, D. 1994b. The crickets of Hawaii: origin, systematics, and evolution. Philadelphia: The Orthoptera Society, 396 pp.

Otte, D. 1995a. Orthoptera Species File, Number 4. Grasshoppers (Acridomorpha) C. Acridoidea (part): A Systematic Catalog. Philadelphia: Philadelphia Academy of Sciences and The Orthoptera Society,

Otte, D. 1995b. Orthoptera Species File, Number 5. Grasshoppers (Acridomorpha) D. Acridoidea (part). A Systematic Catalog. Philadelphia: Philadelphia Academy of Sciences and The Orthoptera Society, 630 pp.

Otte, D. 1997a. Orthoptera Species File, Number 6. Tetrigoidea and Tridactyloidea. A Systematic Catalog. Philadelphia: Philadelphia Academy of Sciences and The Orthoptera Society, 261 pp.

Otte, D. 1997b. Orthoptera Species File, Number 7. Tettigonioidea. A Systematic Catalog. Philadelphia: Philadelphia Academy of Sciences and The Orthoptera Society, 373 pp.

Otte, D. 2000. Orthoptera Species File, Number 8. Gryllacridoidea. A Systematic Catalog. Philadelphia: Philadelphia Academy of Sciences and The Orthoptera Society, 97 pp.

Otte, D., D. C. Eades and P. Naskrecki. 2003. Orthoptera Species File Online (Version 2). http://osf2.orthoptera.org/basic/HomePage.asp

Rentz, D. C. F., and D. B. Weissman. 1981. Faunal affinities, systematics, and bionomics of the Orthoptera of the California Channel Islands. Univ. Calif. Publ. Entomol. 94:1–240.

Vickery, V. R., and D. K. McE. Kevan. 1985. The Grasshoppers, Crickets, and Related Insects of Canada and Adjacent Regions: Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera. The Insects and Arachnids of Canada, Part 14. Ottawa: Canadian Government Publishing Centre, 918 pp.

Vickerey, V. R., and D. E. Johnstone. 1970. Generic status of some Nemobiinae (Orthoptera: Gryllidae) in northern North America. Ann. Entomol. Soc. Amer. 63:1740–1749.

Vickerey, V. R., and D. E. Johnstone. 1973. The Nemobiinae (Orthoptera: Gryllidae) of Canada. Can. Entomol. 105:623–645.

Walker, T. J., and T. E. Moore. 2003. Singing insects of North America. http://buzz.ifas.ufl.edu/

12

Order Phasmatodea[1]

Walkingsticks and Leaf Insects

The members of this order do not have enlarged hind femora (and they do not jump), and the tarsi are usually five-segmented (three-segmented in the Timematidae). The species in North America have an elongated and sticklike body, and the wings are either much reduced or entirely absent. Some tropical forms (leaf insects) are flattened and expanded laterally (and have at least the hind wings well developed), and very greatly resemble leaves. These insects lack tympana and stridulatory organs; the cerci are short and one-segmented; and the ovipositor is short and concealed.

The walkingsticks are slow-moving herbivorous insects that are usually found on trees or shrubs. They are very similar to twigs in appearance, and this mimicry probably has protective value. Walkingsticks can emit a foul-smelling substance from glands in the thorax, a behavior that serves as a means of defense. Unlike most insects, the walkingsticks can regenerate lost legs, at least in part. These insects are usually not numerous enough to do much damage to cultivated plants but, when numerous, may do serious damage to trees.

Some species are parthenogenetic, the males being completely unknown. The eggs are not laid in any particular situation but are simply scattered on the ground. There is a single generation per year, with the egg stage overwintering. The eggs often do not hatch the following spring but hatch the second year after they are laid. For this reason walkingsticks are generally abundant only in alternate years. The young are usually greenish, and the adults are brownish.

The walkingsticks are widely distributed (more than 2000 species worldwide), but the group is most diverse in the tropics, especially in the Indo-Malayan region, and in the Nearctic is better represented in the southern states. All walkingsticks in the United States are wingless except *Aplopus mayeri* Caudell, which occurs in southern Florida. This species has short, oval front wings, and the hind wings project 2 or 3 mm beyond the front wings. Some tropical walkingsticks are around 30 cm or so in length.

Classification of the Phasmatodea

Timematidae (Timemidae)—timema walkingsticks
Pseudophasmatidae (Bacunculidae)—striped walkingsticks
Heteronemiidae—common walkingsticks
Phasmatidae (Bacteriidae)—winged walkingsticks

Key to the Families of Phasmatodea

1.	Tarsi 3-segmented	Timematidae	p. 228
1′.	Tarsi 5-segmented	2	

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[1] This chapter was edited by David A. Nickle.

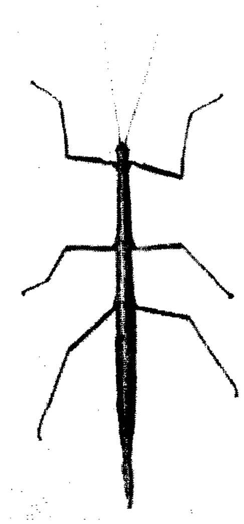
2(1′).	Mesothorax never more than 3 times as long as prothorax; middle and hind tibiae deeply emarginate apically, receiving base of tarsi in repose	Pseudophasmatidae	p. 228
2′.	Mesothorax at least 4 times as long as prothorax; middle and hind tibiae not deeply emarginate apically	3	
3(2′).	Adults with short wings; first abdominal tergum as long as or longer than metanotum (longer than wide); head with 2 stout spines on vertex	Phasmatidae	p. 228
3′.	Wings absent; first abdominal tergum much shorter than metanotum (subquadrate); vertex without stout spines	Heteronemiidae	p. 228

***Family* Timematidae—Timema Walkingsticks:** These insects are much stouter and shorter than most other walkingsticks and somewhat resemble earwigs. They are short-legged, apterous, 15–30 mm in length, and greenish to pink in color. The tarsi are all three-segmented and have unequal pretarsal claws. There are 10 known species, all belonging to the genus *Timema*, which occur in deciduous trees in California, Arizona, and Nevada. At least one species is parthenogenetic. Timemas are usually collected by beating foliage.

***Family* Pseudophasmatidae—Striped Walkingsticks:** In these insects, the tergum of the first abdominal segment is at least as long as the thoracic metanotum, with which it is completely fused, and the middle and hind tibiae are broadly and deeply emarginate apically, receiving the base of the tarsus in repose. They are brownish yellow (male) or brown (female) with a dark median and two lateral dorsal stripes. They have defensive glands from which they can squirt a thick, milky fluid. Our fauna is restricted to two species of *Anisomorpha*, both of which occur in Florida. They are found in grass or on bushes all year long.

***Family* Heteronemiidae—Common Walkingsticks:** These insects are more sticklike than the other three families of Phasmatodea. There are 20 species in six genera in North America; 8 of the species belong to the genus *Diapheromera*. The common walkingstick in the northeastern states is *D. femoratum* (Say) (Figure 12–1), which sometimes becomes abundant enough to seriously defoliate forest trees. This family contains the longest insect in the United States, *Megaphasma denticrus* (Stål), which reaches a length of 150–180 mm. It occurs in the South and Southwest.

***Family* Phasmatidae—Winged Walkingsticks:** There are more than 100 Neotropical species in this family, but only one, *Aplopus mayeri* Caudell, occurs in North America (southern Florida), feeding on bay cedar and other shore vegetation. It is 80–130 mm in length and is the only North American walkingstick with wings. The head has two stout spines on the vertex.



Ohio Agricultural Research and Development Center

Figure 12–1 A walkingstick, *Diapheromera femorata* (Say).

Collecting and Preserving Phasmatodea

Walkingsticks are relatively large and slow-moving and, once found, are fairly easy to collect. The best time for collecting the adults of most species is from midsummer to late fall. Adults should be pinned in about the middle of the body (from front to rear). If the specimen is very soft-bodied, support the body by a piece of cardboard or by pins, or it will sag at either end.

References

Bedford, G. O. 1978. Biology and ecology of the Phasmatodea. Annu. Rev. Entomol. 23:125–149.

Bradley, J. C., and B. S. Galil. 1977. The taxonomic arrangement of the Phasmatodea with keys to the subfamilies and tribes. Proc. Entomol. Soc. Wash. 79:176–208.

Gustafson, J. F. 1966. Biological observations on *Timema californica* (Phasmoidea: Phasmidae). Ann. Entomol. Soc. Amer. 59:59–61.

Helfer, J. R. 1987. How to Know the Grasshoppers, Cockroaches, and Their Allies, 2nd edition. New York: Dover Publications, 363 pp.

Henry, L. M. 1937. Biological notes on *Timema californica* Scudder. Pan-Pac. Entomol. 13:137–141.

Nickle, D. A. 1987. Order Phasmatodea. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 145–146. Dubuque, IA: Kendall/Hunt, 754 pp.; illus.

Sellick, J. T. C. 1997. Descriptive terminology of the phasmid egg capsule, with an extended key to the phasmid genera based on egg structure. Syst. Entomol. 22:97–122.

Strohecker, H. F. 1966. New *Timema* from Nevada and Arizona (Phasmodea: Timemidae). Pan-Pac. Entomol. 42: 25–26.

Tilgner, E. 2000. The fossil record of Phasmida (Insecta: Neoptera). Insect Syst. & Evol. 31:473–480.

Tilgner, E. H., T. G. Kiselyova, and J. V. McHugh. 1999. A morphological study of *Timema cristinae* Vickery with implications for the phylogenetics of Phasmida. Deutsch. Entomol. Z. 46:149–162.

Vickery, V.R. 1993. Revision of *Timema* Scudder (Phasmatoptera: Timematodea) including three new species. Can. Entomol. 125: 657–692.

Vickery, V. R., and D. K. McE. Kevan. 1985. The Grasshoppers, Crickets, and Related Insects of Canada and Adjacent Regions. Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera. The Insects and Arachnids of Canada, Part 14. Ottawa: Canadian Government Publishing Centre, 918 pp.

13

Order Grylloblattodea

Rock Crawlers

The first member of this group was not discovered until 1914, when Walker described *Grylloblatta campodeiformis* from Banff, Alberta. Rock crawlers are slender, elongate, wingless insects, usually about 15–30 mm in length (Figure 13–1). The body is pale in color and finely pubescent. The eyes are small or absent, and there are no ocelli. The antennae are long and filiform, consisting of 23 to 45 segments; the cerci are long, with either 5 or 8 segments; and the sword–shaped ovipositor of the female is nearly as long as the cerci.

There are only 25 species and four genera of living rock crawlers in the world (Japan, Siberia, China, Korea, northwestern United States and western Canada). Eleven species, all belonging to the genus *Grylloblatta* in the family Grylloblattidae, have been described from North America.

Rock crawlers live in cold places such as the talus slopes at the edges of glaciers and in ice caves, often at high elevations. They are mainly nocturnal, and their principal food appears to be dead insects and other organic matter found on the snow and ice fields. They are soft-bodied, and probably best preserved in alcohol.

Some specialists consider grylloblattids to be living remnants of the extinct order Protorthoptera, and some still consider them merely a disjunctive, primitive subfamily of Orthoptera, a notion not too difficult to accept. Wheeler et al. (2001) proposed on the basis of morphological and molecular evidence that they are most closely related to the Dermaptera.

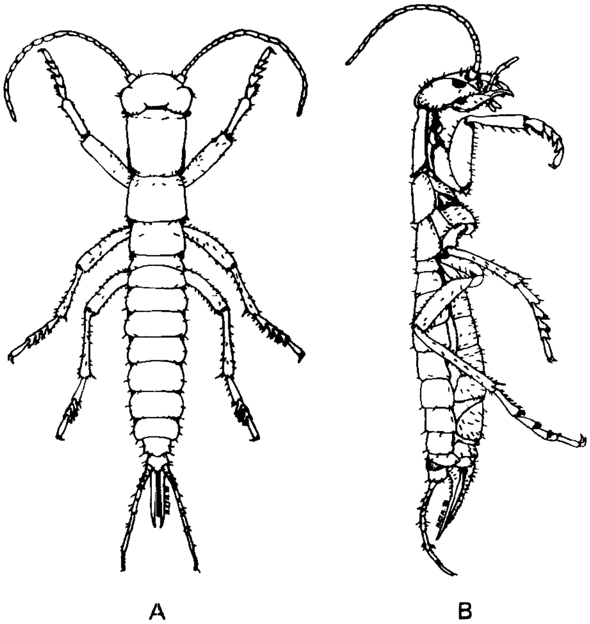


Figure 13–1 A rock crawler, *Grylloblatta* sp. A, dorsal view; B, lateral view.

References

Ando, H. 1982. Biology of the Notoptera. Nagano, Japan: Kashiyo-Insatsu, 194 pp.

Gurney, A. B. 1948. The taxonomy and distribution of the Grylloblattidae. Proc. Entomol. Soc. Wash. 50:86–102.

Gurney, A. B. 1953. Recent advances in the taxonomy and distribution of *Grylloblatta* (Orthoptera: Grylloblattidae). J. Wash. Acad. Sci. 43:325–332.

Gurney, A. B. 1961. Further advances in the taxonomy and distribution of *Grylloblatta* (Orthoptera: Grylloblattidae). Proc. Biol. Soc. Wash. 74:67–76.

Helfer, J. R. 1987. How to Know the Grasshoppers, Cockroaches, and Their Allies. Dubuque, IA: William C Brown, 363 pp.

Kamp, J. W. 1963. Descriptions of two new species of Grylloblattidae and the adult of *Grylloblatta barberi*, with an interpretation of their geographic distribution. Ann. Entomol. Soc. Amer. 56:53–68.

Kamp, J. W. 1970. The cavernicolous Grylloblattoidea of the western United States. Ann. Speleology 25:223–230.

Kamp, J. W. 1973. Taxonomy, distribution and zoogeographic evolution of *Grylloblatta* in Canada (Insecta: Notoptera). Can. Entomol. 105:1235–1249.

Nickle, D. A. 1987. Order Grylloblattodea (Notoptera). In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 143–144. Dubuque, IA: Kendall/Hunt, 754 pp.

Rentz, D. C. F. 1982. A review of the systematics, distribution and bionomics of the North American Grylloblattidae. In H. Ando. (Ed.), Biology of the Notoptera. Nagano, Japan: Kashiyo-Insatsu, 194 pp.

Vickery, V. R., and D. K. McE. Kevan. 1985. The Grasshoppers, Crickets, and Related Insects of Canada and Adjacent Regions: Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera; The Insects and Arachnids of Canada, Part 14. Ottawa: Canadian Government Publishing Centre, 918 pp.

Walker, E. M. 1914. A new species of Orthoptera, forming a new genus and family. Can. Entomol. 46:93–99.

Wheeler, W. C., M. Whiting, Q. D. Wheeler, and J. M. Carpenter. 2001. The phylogeny of the extant hexapod orders. Cladistics 17:113–169.

14

Order Mantophasmatodea[1]

The Mantophasmatodea is the newest addition to the cast of insect orders. The genus *Raptophasma* was first described in 2001 for fossil specimens preserved in Baltic amber, approximately 30 million years old (Zompro 2001). Specimens of similar species were later discovered in collections from Namibia and Tanzania in Africa (Figure 14–1), and a new order was proposed for them. Mantophasmatodea have since been found in a number of locations in South Africa in the Cape Faunal Zone (Figure 14–2), an area well known for species richness and endemism. The order contains only a single family, Mantophasmatidae, and three genera: the fossil *Raptophasma* (one described species) and the living genera *Mantophasma* (two species) and *Praedatophasma* (one species). Researchers think there are at least three new species in South Africa.

Mantophasmatodea are rather small, generally 2–3 cm in length, and both sexes are wingless. They have chewing mouthparts, the head is hypognathous, and the antennae are long and filiform. The tarsi are five-segmented. They have simple metamorphosis. According to van Noort (2003), Mantophasmatodea superficially resemble immature mantids, but the fore legs are not modified for prey capture. Nevertheless, these are predatory insects. Adults are rather short-lived, surviving for only a few weeks.

In the original description of the order, it was unclear which order(s) of insects were the closest relatives of Mantophasmatodea, but Grylloblattodea and Phasmatodea were suggested as possibilities. Unfortunately, no phylogenetic analysis preceded the description. It is unclear, at this early point, whether the recognition of this group as an order will meet with general acceptance or if it will eventually be subsumed within Grylloblattodea or another group.

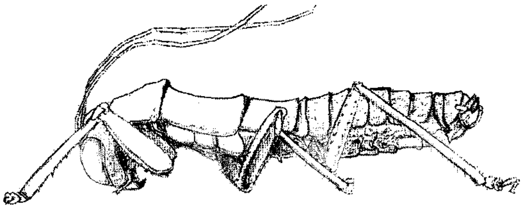


Figure 14–1 *Praedatophasma maraisi* Zompro & Adis, female, lateral view; antennae are not completely shown. (Reproduced with permission of Thom Glas.)

Simon van Noort/Iziko Museums of Cape Town

Figure 14–2 An undescribed species of Mantophasmatodea from South Africa.

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[1] Mantophasmatodea: a combination of *Mantis* (Mantodea) and *Phasma* (Phasmatodea), referring to the purported similarity to those two orders.

References

Arillo, A., V. M. Ortuño, and A. Nel. 1997. Description of an enigmatic insect from Baltic amber. Bull. Soc. Entomol. France 102:11–14.

Klass, K.-D., O. Zompro, N. P. Kristensen, and J. Adis. 2002. Mantophasmatodea: A new insect order with extant members in the Afrotropics. Science 296:1456–1459.

Picker, M. D., J. F. Colville, and S. van Noort. 2002. Mantophasmatodea now in South Afrika. Science 297:1475.

van Noort, S. 2003. Order Mantophasmatodea (mantos). Available on the Web at www.museums.org.za/bio/insects/mantophasmatodea/ 10 Dec., 2003.

Zompro, O. 2001. The Phasmatodea and *Raptophasma* n. gen., Orthoptera incertae sedis, in Baltic amber (Insecta: Orthoptera). Mitt. Geol.-Paläontol. Inst. Univ. Hamburg 85: 229–261.

Zompro, O., J. Adis, and W. Weitschat. 2002. A review of the order Mantophasmatodea (Insecta). Zoologischer Anzeiger 241(3): 269–279.

15

Order Dermaptera[1]
Earwigs

Earwigs are elongate, slender, somewhat flattened insects that resemble rove beetles but have forcepslike cerci (Figure 15–1). Adults may be winged or wingless, with one or two pairs of wings. If winged, the front wings are short, leathery, and veinless (and are usually called *tegmina* or *elytra*), and the hind wings (when present) are membranous and rounded, with radiating veins. At rest the hind wings are folded beneath the front wings with only the tips projecting. The tarsi have three segments, the mouthparts are of the chewing type, and the metamorphosis is simple.

Immature earwigs have fewer antennal segments than do adults, with segments added at each molt. Immatures can be distinguished from adults by the combination of a malelike 10-segmented abdomen (adult females have only 8 apparent segments) with femalelike straight forceps (adult male forceps usually have the inner margin distinctly curved) (Figure 15–2).

Earwigs are largely nocturnal in habit and hide during the day in cracks, in crevices, under bark, and in debris. They feed mainly on dead and decaying vegetable matter, but some occasionally feed on living plants, and a few are predaceous.

Some of the winged forms are good fliers, but others fly only rarely. The eggs are laid in burrows in the ground or in debris, generally in clusters, and are guarded by the female until they hatch. Earwigs overwinter in the adult stage.

Some species of earwigs have glands opening on the dorsal side of the third and fourth abdominal segments, from which they emit a foul-smelling fluid that serves as a means of protection. Some species can squirt this fluid 75–100 mm.

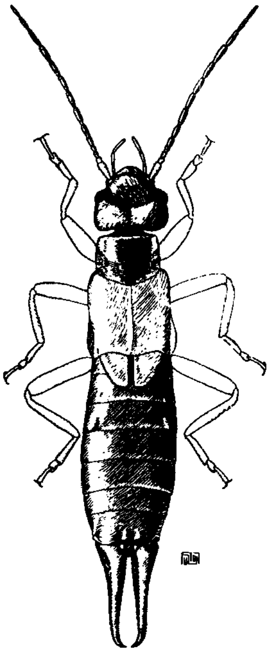

Figure 15–1 The European earwig, *Forficula auricularia* L., female, about 4×. (Courtesy of Fulton and the Oregon Agricultural Experiment Station.)

The name "earwig" is derived from an old superstition that these insects enter people's ears. This belief is entirely without foundation. Earwigs do not bite but, if handled, will attempt to pinch with their cerci, and

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[1] Dermaptera: *derma*, skin; *ptera*, wings (referring to the texture of the front wings).

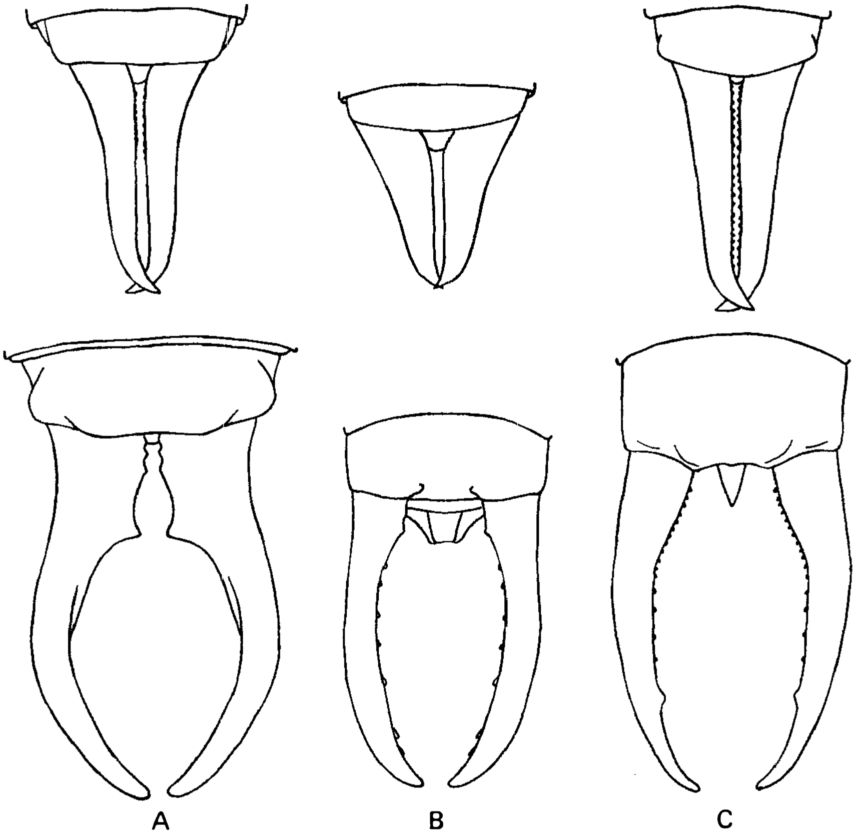


Figure 15–2 Anal forceps of Dermaptera. A, *Forficula auricularia* L.; B, *Labia minor* (L.); C, *Doru lineare* (Eschscholtz). Upper figures, forceps of female; lower figures, forceps of male.

the abdomen is quite maneuverable. The larger earwigs, especially the males, can inflict a painful pinch.

Classification of the Dermaptera

The order Dermaptera is usually divided into three suborders, the Arixenina, the Diploglossata (Hemimerina), and the Forficulina. Some authorities consider the Arixenina a family (Arixenidae) of the Forficulina. The Arixenina are Malayan ectoparasites of bats, and the Diploglossata are South African parasites of rodents. The Forficulina is the only suborder occurring in North America. Of the 22 North American earwig species, 12 have been introduced from Europe or from the tropics. Our species represent six families, adults of which may be separated by the following key.

Key to the Families of Dermaptera

1. Second tarsal segment extending distally beneath base of third (Figure 15–3D); antennae with 12–16 segments 2

1′. Second tarsal segment not extending distally beneath base of third (Figure 15–3C); antennae with 10–31 segments 3

2(1). Distal extension of second tarsal segment dilated, broader than third segment (Figure 15–3D), and without a dense brush of hairs beneath; antennae with 12–16 segments; usually yellowish or brownish; widely distributed Forficulidae p. 237

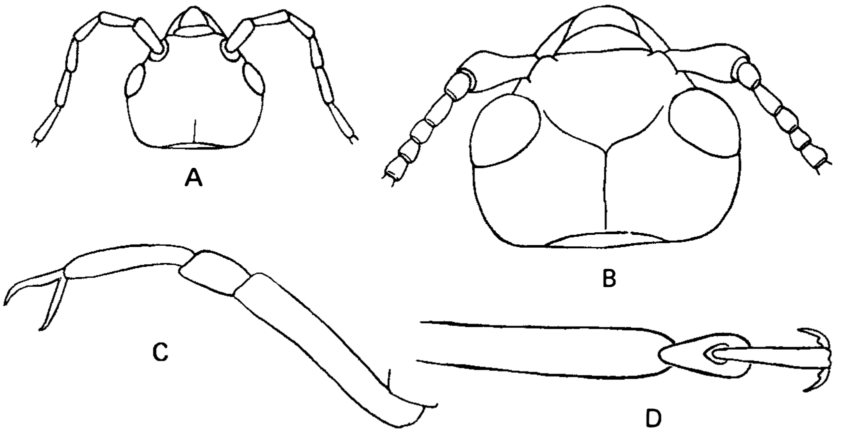


Figure 15–3 Characters of the Dermaptera. A, head of *Labia minor* (L.), dorsal view; B, head of *Labidura riparia* Pallas, dorsal view; C, tarsus of *Labidura*; D, tarsus of *Forficula*.

2′.	Distal extension of second tarsal segment not dilated, no wider than third segment, and with dense brush of hairs beneath; antennae 12-segmented; black; California	Chelisochidae	p. 237
3(1′).	A large, padlike arolium between tarsal claws; male forceps curved strongly inward; recorded near Miami, Florida	Pygidicranidae	p. 236
3′.	No arolium between tarsal claws; male forceps not strongly curved (Figure 15–2B,C); widely distributed	4	
4(3′).	Antennae with 25–30 segments; pronotum light brown with 2 dark longitudinal stripes; length 20–30 mm; southern United States, from North Carolina to Florida and California	Labiduridae	p. 237
4′.	Antennae with 10–24 segments; pronotum uniformly colored; length 4–25 mm; widely distributed	5	
5(4′).	Antennae with 14–24 segments; tegmina present as rounded flaps not meeting at inner basal margins, or absent; right forceps of male more strongly curved than left; length 9–25 mm	Anisolabididae	p. 236
5′.	Antennae with 10–16 segments; tegmina normally developed and meeting along entire midline; male forceps symmetrical; length less than 20 mm	Labiidae	p. 237

Family **Pygidicranidae:** This family is represented in the United States by a single species, *Pyragropsis buscki* (Caudell), which is fully winged and 12–14 mm in length. This insect has been collected in southern Florida and also occurs in Cuba, Jamaica, and Hispaniola.

Family **Anisolabididae (Carcinophoridae, Psalididae, Anisolabidae; Labiduridae in part)—Seaside and Ring-Legged Earwigs:** The seaside earwig, *Anisolabis maritima* (Bonelli), is a wingless, blackish brown insect 20–25 mm in length with 20–24 antennal segments. It is an introduced species that is predaceous and usually found beneath debris along seashores. It now occurs locally along the Atlantic, Pacific, and Gulf Coasts. The genus *Euborellia* contains six North American species, which are 9–18 mm in length with 14–20 antennal segments. These earwigs are usually found in debris and occur mainly in the southern states. The most common species is the ring-legged earwig, *E. annulipes* (Lucas), a wingless species that is widely distributed and sometimes invades houses. *Euborellia cincticollis* (Gerstaecker) was introduced into California and Arizona. This species has three morphs, with individuals exhibiting well-developed wings, shortened front wings with the hind wings reduced or absent, or lacking both pairs of wings altogether.

Family **Labiidae—Little Earwigs:** This family contains eight North American species in three genera, with the most common species being *Labia minor* (L.), an introduced species. This insect is 4–7 mm in length and covered with golden hair. It is a good flier and can be found flying during the early evening or attracted to lights at night. *Marava pulchella* (Audinet-Serville) is a larger (8–10 mm in length), shining reddish brown species in which individuals can possess either well-developed wings or short front wings with the hind wings reduced or absent. This insect is found in the southern states. The genus *Vostox* contains three species, one of which, *V. apicedentatus* (Caudell), is 9–12 mm in length and fairly common around dead leaves and cacti in the desert regions of the Southwest.

Family **Labiduridae—Striped Earwigs:** This group includes a single North American species, *Labidura riparia* (Pallas), an introduced species that occurs in the southern part of the United States, from North Carolina south to Florida and west to California. This species is most readily recognized by its large size (length 20–30 mm) and the longitudinal dark stripes on the pronotum and tegmina. It is nocturnal and predaceous, hiding under debris during the day.

Family **Chelisochidae—Black Earwigs:** This group includes a single North American species, *Chelisoches morio* (Fabricius), which is a native of the tropics (islands in the Pacific) but has become established in California. This insect is black and 16–20 mm long.

Family **Forficulidae—European and Spine-tailed Earwigs:** The most common member of this family is the European earwig, *Forficula auricularia* L., a brownish black insect 15–20 mm long (Figure 15–1). It is widely distributed throughout southern Canada south to North Carolina, Arizona, and California. It occasionally causes substantial damage to vegetable crops, cereals, fruit trees, and ornamental plants. The spine-tailed earwigs (*Doru*) are a little smaller (12–18 mm in length), and are so called because the male has a short median spine on the terminal abdominal segment (Figure 15–2C).

Collecting and Preserving Dermaptera

Earwigs generally must be looked for in various protected places: in debris, in cracks and crevices, under bark, and about the roots of grasses and sedges. They are not often collected with a net. Some will come to lights at night, and some can be taken in pitfall traps (Figure 35–6A). They are normally preserved dry, on either pins or points. If pinned, they are pinned through the right tegmen, as are beetles.

References

Blatchley, W. S. 1920. Orthoptera of Northeastern America. Indianapolis: Nature, 784 pp.

Brindle, A. 1966. A revision of the subfamily Labidurinae (Dermaptera: Labiduridae). Ann. Mag. Nat. Hist. (13)9:239–269.

Brindle, A. 1971a. A revision of the Labiidae (Dermaptera) of the Neotropical and Nearctic regions. II. Geracinae and Labiinae. J. Nat. Hist. 5:155–182.

Brindle, A. 1971b. A revision of the Labiidae (Dermaptera) of the Neotropical and Nearctic regions. III. Spongiphorinae. J. Nat. Hist. 5:521–568.

Brindle, A. 1971c. The Dermaptera of the Caribbean. Stud. Fauna Curaçao and Other Caribbean Islands 38:1–75.

Brindle, A. 1987. Order Dermaptera. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 171–178. Dubuque, IA: Kendall/Hunt, 754 pp.

Cantrell, I. J. 1968. An annotated list of the Dermaptera, Dictyoptera, Phasmatoptera, and Orthoptera of Michigan. Mich. Entomol. 1:299–346.

Eisner, T. 1960. Defense mechanisms of arthropods. II. The chemical and mechanical weapons of an earwig. Psyche 67:62–70.

Giles, E. T. 1963. The comparative external morphology and affinities of the Dermaptera. Trans. Roy. Entomol. Soc. Lond. 115:95–164.

Gurney, A. B. 1972. Important recent name changes among earwigs of the genus *Doru* (Dermaptera, Forficulidae). Coop. Econ. Insect Rep. (USDA) 22(13):182–185.

Haas, F. 1995. The phylogeny of the Forficulina, a suborder of the Dermaptera. Syst. Entomol. 20:85–98.

Haas, F., and J. Kukalová-Peck. 2001. Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). Eur. J. Entomol. 98:445–509.

Hebard, M. 1934. The Dermaptera and Orthoptera of Illinois. Ill. Nat. Hist. Surv. Bull. 20(3):125–279.

Helfer, J. R. 1987. How to Know the Grasshoppers, Cockroaches, and Their Allies, 2nd ed. New York: Dover Publications, 363 pp.

Hinks, W. D. 1955–1959. A Systematic Monograph of the Dermaptera of the World Based on Material in the British Museum (Natural History). Part I: Pygidicranidae, Subfamily Diplatyinae, 132 pp. (1955). Part II: Pygidicranidae Excluding Diplatyinae, 218 pp. (1959). London: British Museum (Natural History).

Hoffman, K. M. 1987. Earwigs (Dermaptera) of South Carolina, with a key to the eastern North American species and a checklist of the North American fauna. Proc. Ent. Soc. Wash. 89:1–14.

Knabke, J. J., and A. A. Grigarick. 1971. Biology of the African earwig, *Euborellia cincticollis* (Gerstaecker) in California and comparative notes on ***Euborellia annulipes*** (Lucas). Hilgardia 41:157–194.

Langston, R. L., and J. A. Powell. 1975. The earwigs of California. Bull. Calif. Insect Surv. 20:1–25.

Popham, E. J. 1965. A key to the Dermaptera subfamilies. Entomologist 98:126–136.

Popham, E. J. 1965. Towards a natural classification of the Dermaptera. Proc. 12th Int. Congr. Entomol. Lond. (1964): 114–115.

Popham, E. J. 1985. The mutual affinities of the major earwig taxa (Insecta, Dermaptera). Z. Zool. Syst. Evol.-Forsch. 23:199–214.

Steinmann, H. 1978. A systematic survey of the species belonging to the genus *Labidura* Leach, 1815 (Dermaptera). Acta Zool. Acad. Sci. Hung. 25:415–423.

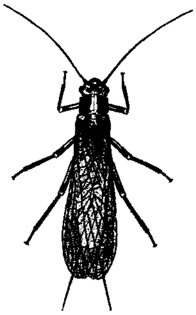
Steinmann, H. 1989. World Catalog of Dermaptera. Series Entomologica 43:1–934.

Vickery, V. R., and D. K. McE. Kevan. 1985. The Grasshoppers, Crickets, and Related Insects of Canada and Adjacent Regions: Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera. The Insects and Arachnids of Canada, Part 14. Ottawa: Canadian Government Publishing Centre, 918 pp.

16

Order Plecoptera[1,2]

Stoneflies



Stoneflies are mostly medium-sized or small, somewhat flattened, soft-bodied, rather drab-colored insects found near streams or rocky lake shores. They are generally poor fliers and are seldom found far from water. Most species have four membranous wings (Figure 16–1). The front wings are elongate and rather narrow and usually have a series of crossveins between M and Cu_1 and between Cu_1 and Cu_2. The hind wings are slightly shorter than the front wings and usually have a well-developed anal lobe that is folded fanwise when the wings are at rest. A few species of stoneflies have reduced wings or lack wings, usually in the male. Stoneflies at rest hold the wings flat over the abdomen (Figure 16–2A). The antennae are long, slender, and many-segmented. The tarsi are three-segmented. Cerci are present and may be long or short. The mouthparts are of the chewing type, although in many adults (which do not feed) they are somewhat reduced. The stoneflies undergo simple metamorphosis, and the nymphal stages of development are aquatic.

Stonefly nymphs (Figures 16–2B and 16–3) are somewhat elongate, flattened insects with long antennae and long cerci, and often with branched gills on the thorax and about the bases of the legs. They are very similar to mayfly nymphs but lack a median caudal filament; that is, they have only two tails, whereas mayfly nymphs nearly always have three. Stonefly nymphs have two tarsal claws and mayfly nymphs have only one, and the gills are different: Mayfly nymphs have leaflike gills along the sides of the abdomen (Figure 9–2), whereas stonefly gills are always fingerlike, either simple or branched, and only occur ventrally (Figure 16–2B). Stonefly nymphs are often found under stones in streams or along lake shores (hence the common name of these insects), but may occasionally be found anywhere in a stream where food is available. A few species live in underground water, and their nymphs sometimes appear in wells or other drinking water supplies. Some species are plant feeders in the nymphal stage, and others are predaceous or omnivorous. Some species of stoneflies emerge, feed, and mate during the fall and winter months. The nymphs of these species are generally plant feeders, and the adults feed chiefly on blue-green algae and are diurnal in feeding habits. The species that emerge during the summer vary in nymphal feeding habits. Many do not feed as adults.

In many species of stoneflies, the sexes get together in response to acoustic signals. The males drum by tapping the tip of the abdomen on the substrate. Virgin females respond to this drumming, and answer with a drumming of their own either during or immediately after the male drumming. The males drum throughout their adult life, and the signals are species specific.

Classification of the Plecoptera

This order in North America is divided into two groups. Previously they were separated simply by the structure of the labium, comparing the length of the glossae and paraglossae (Figure 16–4). However,

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[1] Plecoptera: *pleco*, folded or plaited; *ptera*, wings (referring to the fact that the anal region of the hind wings is folded when the wings are at rest).

[2] This chapter was edited by Richard W. Bauman.

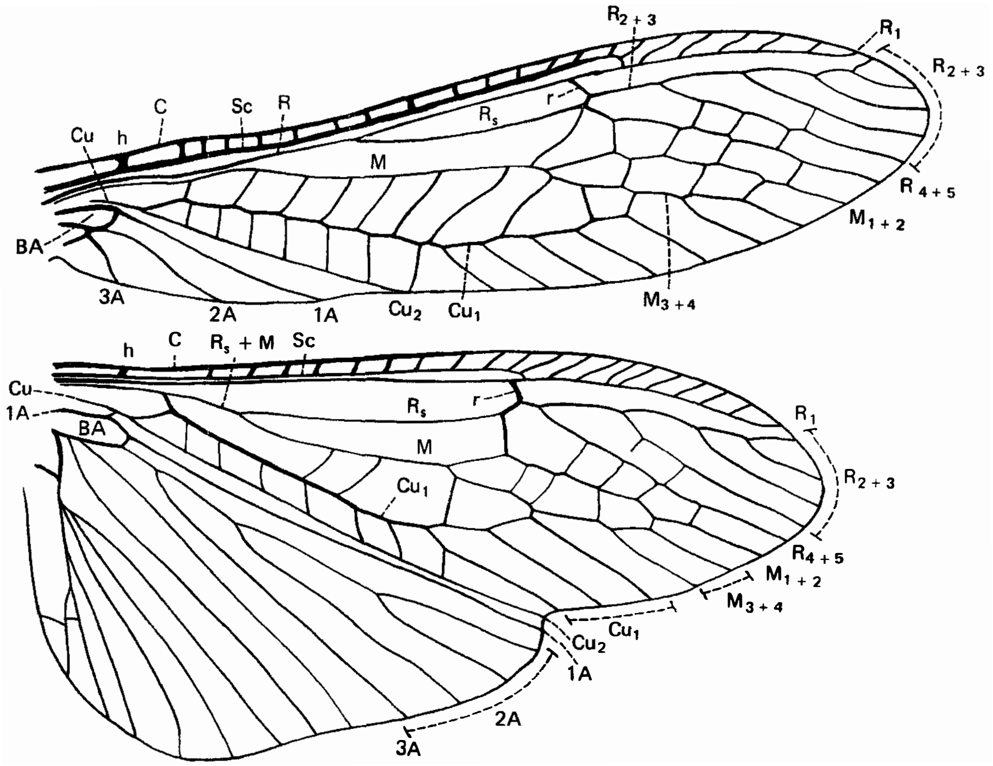

Figure 16–1 Wings of a perlid stonefly. *BA*, basal anal cell.

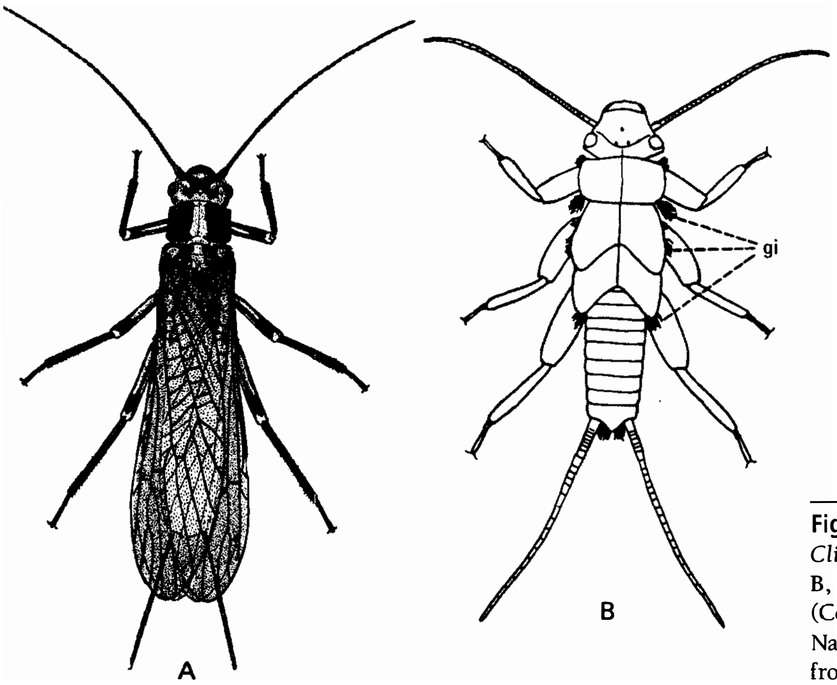

Figure 16–2 A, an adult stonefly, *Clioperla clio* Newman (Perlodidae); B, a stonefly nymph. *gi*, gills. (Courtesy of Frison and the Illinois Natural Nistory Survey; B redrawn from Frison.)

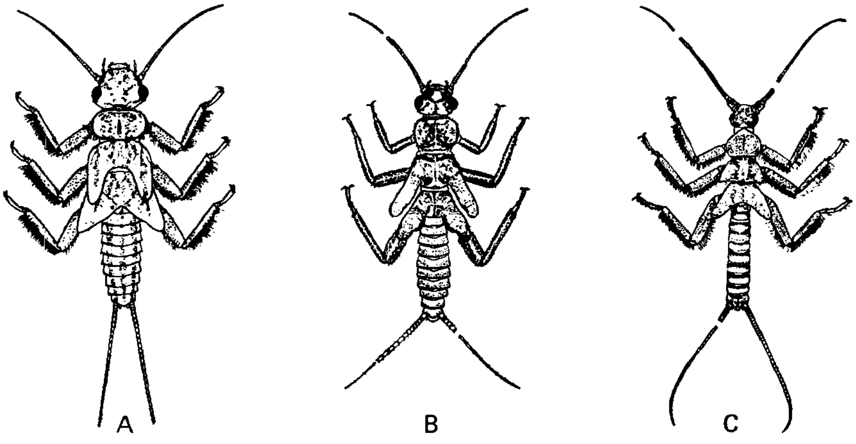

Figure 16–3 Stonefly nymphs. A, *Isoperla transmarina* (Newman) (Perlodidae); B, *Nemoura trispinosa* Claassen (Nemouridae); C, *Oemopteryx glacialis* (Newport) (Taeniopterygidae). (Courtesy of Harden and the Entomological Society of America.)

Zwick (1973) showed that the families Pteronarcyidae and Peltoperlidae belong in the group Systellognatha. He noted that the structure of the labium is a function of feeding method, with herbivores exhibiting similarly sized glossae and paraglossae, and carnivores having them modified in size and shape.

Different authorities recognize different numbers of families; we follow here the arrangement of Stark et al. (1986), who recognize nine families in North America. This arrangement is outlined next, with alternate names and arrangements in parentheses. The numbers in parentheses, representing the numbers of North American species, are from Stark et al. (1986).

- Group Euholognatha (Filipalpia, Holognatha) (280)
  - Taeniopterygidae (Nemouridae in part) (33)—winter stoneflies
  - Nemouridae (Nemourinae of Nemouridae) (64)—spring stoneflies
  - Leuctridae (Nemouridae in part) (52)—rolled-wing stoneflies
  - Capniidae (Nemouridae in part) (131)—small winter stoneflies
- Group Systellognatha (Setipalpia, Subulipalpia) (257)
  - Pteronarcyidae (Pteronarcidae) (10)—giant stoneflies
  - Peltoperlidae (17)—roachlike stoneflies
  - Perlidae (44)—common stoneflies
  - Perlodidae (including Isoperlidae) (114)
  - Chloroperlidae (72)—green stoneflies

The principal characters used to separate the families of stoneflies are wing venation, characters of the

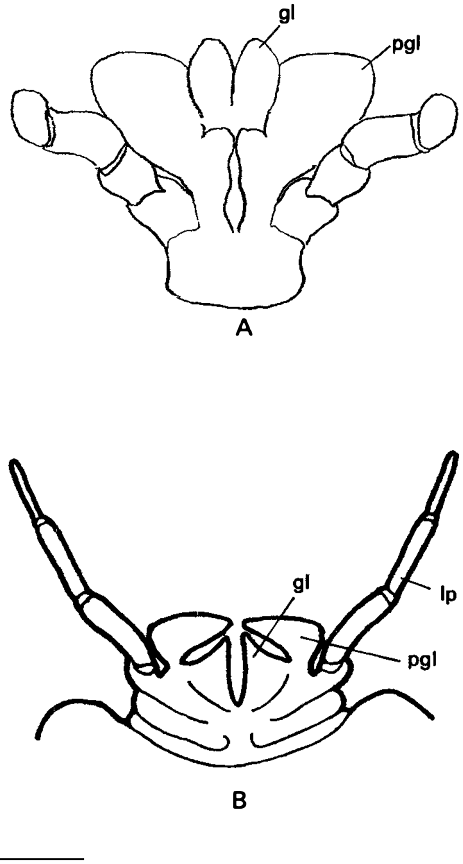

Figure 16–4 Labia of adult stoneflies, ventral views. A, *Taeniopteryx nivalis* (Fitch) (Taeniopterygidae); B, *Perla* (Perlidae). *gl*, glossa; *lp*, labial palp; *pgl*, paraglossa.

tarsi, the gill remnants, and adult mouthparts. The gill remnants are usually shriveled and difficult to see in pinned and dried specimens. Their location on the thorax is shown in Figure 16–5. The characters of the gill remnants are much easier to study in specimens that are preserved in alcohol.

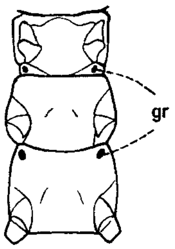

Figure 16–5 Thorax of *Acroneuria* (Perlidae), ventral view. *gr*, gill remnants. (Redrawn from Frison, courtesy of the Illinois Natural History Survey.)

Key to the Families of Plecoptera

Keys to nymphs are given by Claassen (1931), Jewett (1956), Pennak (1978), Harper (1984), Stewart and Stark (1984, 1988), and Baumann (1987).

1.	Labium with glossae and paraglossae about the same size, labium thus appearing to have 4 similar terminal lobes (Figure 16–4A)	2	
1′.	Labium with glossae very small, appearing to have 2 terminal lobes (the paraglossae), each with a small basomesal lobe (the glossae) (Figure 16–4B)	7	
2(1).	Basal tarsal segment short, much shorter than third segment (Figure 16–6E)	3	
2′.	Basal tarsal segment longer, nearly as long as or longer than third segment (Figure 16–6A–D)	4	
3(2).	Anal area of front wing with 2 series of crossveins (Figure 16–7A); head with 3 ocelli; gill remnants on sides of first 2 or 3 abdominal segments; large stoneflies, usually over 25 mm in length	**Pteronarcyidae**	**p. 245**

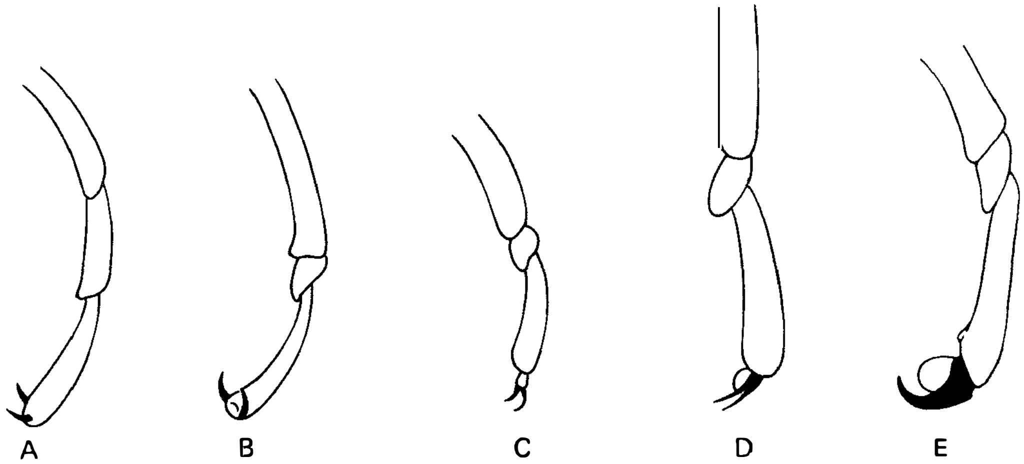

Figure 16–6 Hind tarsi of Plecoptera. A, *Taeniopteryx* (Taeniopterygidae); B, *Leuctra* (Leuctridae); C, *Nemoura* (Nemouridae); D, *Allocapnia* (Capniidae); E, *Pteronarcys* (Pteronarcyidae).

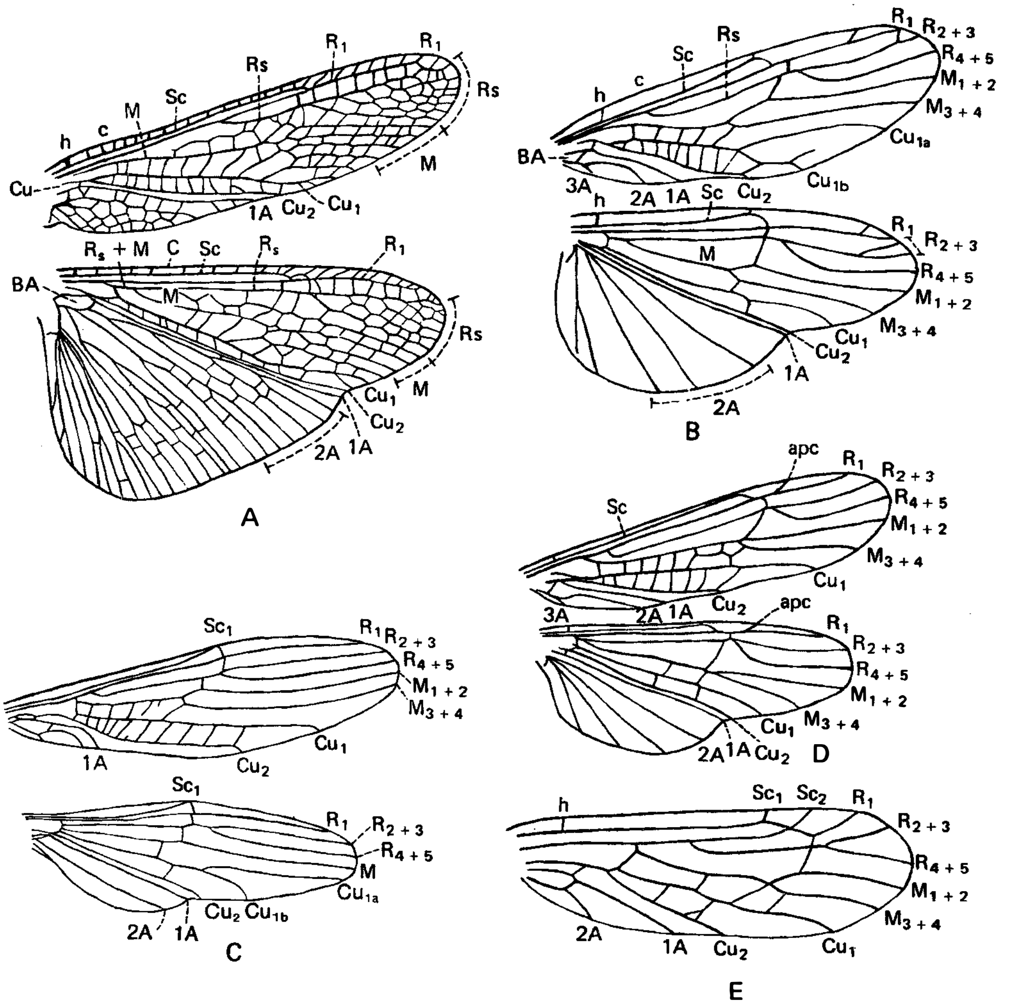

Figure 16–7 Wings of Plecoptera. A, *Pteronarcys* (Pteronarcyidae); B, *Taenionema* (Taeniopterygidae); C, *Leuctra* (Leuctridae); D, *Nemoura* (Nemouridae); E, front wing of a capniid. *apc*, apical crossvein; *BA*, basal anal cell.

3′.	Anal area of front wing with no rows of crossveins (Figure 16–7B–E); head with 2 ocelli; no gill remnants on abdominal segments; length less than 25 mm	Peltoperlidae	p. 245
4(2′).	Second segment of tarsi about as long as each of the other 2 segments (Figure 16–6A)	Taeniopterygidae	p. 244
4′.	Second segment of tarsi much shorter than each of the other 2 segments (Figure 16–6B–D)	5	
5(4′).	Cerci short and 1-segmented; front wing with 4 or more cubital crossveins, 2A forked (Figure 16–7C)	6	
5′.	Cerci long and with 4 or more segments; front wing with only 1 or 2 cubital crossveins, 2A not forked (Figure 16–7E)	Capniidae	p. 245
6(5).	Front wings flat at rest, with an apical crossvein (Figure 16–7D, apc)	Nemouridae	p. 244

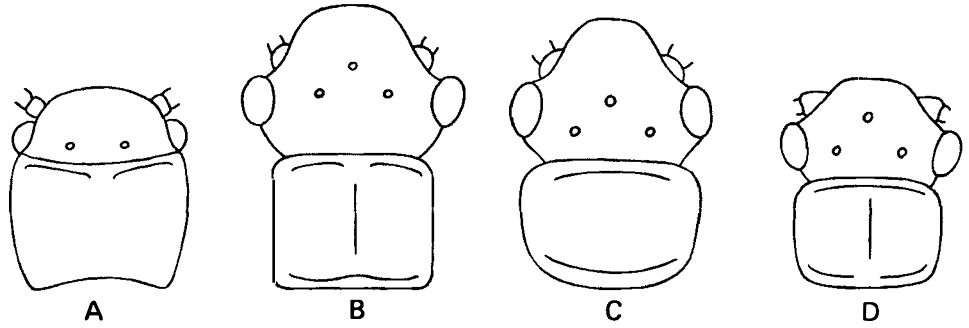

Figure 16–8 Head and pronotum of Plecoptera. A, *Peltoperla* (Peltoperlidae); B, *Isogenoides* (Perlodidae); C, *Chloroperla* (Chloroperlidae); D, *Isoperla* (Perlodidae). (Redrawn from Frison, courtesy of the Illinois Natural History Survey.)

6′.	Front wings at rest bent down around sides of abdomen, without an apical crossvein (Figure 16–7C)	Leuctridae	p. 244
7(1′).	Front wing with cu-a (if present) opposite basal anal cell, or distad of it by no more than its own length; remnants of branched gills on thorax (Figure 16–5)	Perlidae	p. 245
7′.	Front wing with cu-a (if present) usually distad of basal anal cell by more than its own length; no remnants of branched gills on thorax (some Perlodidae may have remnants of unbranched or fingerlike gills on thorax)	8	
8(7′).	Hind wings with anal lobe well developed, with 5–10 anal veins; front wing with no forked vein arising from basal anal cell; pronotum rectangular, the corners acute or narrowly rounded (Figure 16–8B,D); length 6–25 mm	Perlodidae	p. 245
8′.	Hind wings with anal lobe reduced (rarely absent), and usually with no more than 4 anal veins; front wing sometimes with forked vein arising from basal anal cell; pronotum with corners rounded (Figure 16–8C); length 15 mm or less	Chloroperlidae	p. 245

GROUP **Euholognatha:** These stoneflies have the glossae and paraglossae similar in size (Figure 16–4A). They are principally plant feeders, both as adults and nymphs. This is the larger of the two groups, and contains about three fifths of the North American species.

Family **Taeniopterygidae—Winter Stoneflies:** The members of this family are dark brown to black insects, generally 13 mm or less in length, which emerge from January to June. The nymphs (Figure 16–3C) are phytophagous and occur in large streams and rivers. Some adults are flower feeders. Two common eastern species in this group are *Taeniopteryx maura* (Pictet), 8–12 mm in length, which emerges from January to March, and *Strophopteryx fasciata* (Burmeister), 10–15 mm in length, which emerges during March and April.

Family **Nemouridae—Spring Stoneflies:** The adults of this family are brown or black and appear from April to June. The nymphs (Figure 16–3B) are plant feeders, and usually occur in small streams with rocky bottoms.

Family **Leuctridae—Rolled-Wing Stoneflies:** These stoneflies are for the most part 10 mm long or less and brown or black. The wings at rest are bent down over the sides of the abdomen. These insects are most common in hilly or mountainous regions, and the nymphs usually occur in small streams. The adults appear from March to December.

Family **Capniidae—Small Winter Stoneflies:** This is the largest family in the order, and its members, which are blackish and mostly 10 mm long or less, emerge during the winter months. The wings are short or rudimentary in some species. Most of the capniids occurring in the East belong to the genus *Allocapnia*.

Group **Systellognatha:** The carnivorous families Perlidae, Perlodidae and Chloroperlidae have enlarged glossae and small paraglossae. The herbivorous families Pteronarcyidae and Peltoperlidae have these labial lobes of nearly equal size and shape.

Family **Pteronarcyidae—Giant Stoneflies:** This family includes the largest insects in the order; females of a common eastern species, *Pteronarcys dorsata* (Say), may sometimes reach a length (measured to the wing tips) of 55 mm. The nymphs are plant feeders and occur in medium-sized to large rivers. The adults are nocturnal in habit and often come to lights. Adults do not feed. They appear in late spring to early summer.

Family **Peltoperlidae—Roachlike Stoneflies:** This family is so called because the nymphs are somewhat cockroachlike in appearance. Most of these stoneflies are western or northern in distribution. The most common eastern species are brown and 12–18 mm long.

Family **Perlidae—Common Stoneflies:** This family contains the stoneflies most often collected. The adults are nonfeeding spring and summer forms, and most are 20–40 mm long. The nymphs are mostly predaceous.

Two eastern species in this family have only two ocelli, *Perlinella ephyre* (Newman) and *Neoperla clymene* (Newman). Both are about 12 mm in length and brown, with somewhat grey wings. *Neoperla clymene* has ocelli that are close together, and *P. ephyre* has them far apart. *Perlinella drymo* (Newman), 10–20 mm in length, is brown, with two black spots on the yellow head, and it has a row of crossveins in the anal area of the front wing. *Perlesta placida* (Hagen), 9–14 mm long and nocturnal in habit, and *Agnetina capitata* (Pictet), 14–24 mm long and diurnal in habit, have the costal edge of the front wing yellow. One of the largest and most common genera is *Acroneuria*. The adults in this genus are relatively large (20–40 mm long), and the males have a disklike structure in the middle of the posterior portion of the ninth abdominal sternum.

Family **Perlodidae:** The most common members of this family (Figure 16–2A) usually have green wings and yellow or green body, and are 6–15 mm in length. Most adults do not feed, but members of the subfamily Isoperlinae seem to be chiefly pollen feeders. They are diurnal in habit. Other less common species are brown or black and 10–25 mm long. The nymphs are omnivores or carnivores.

Family **Chloroperlidae—Green Stoneflies:** The adults of this family are 6–15 mm long and yellow or green. They appear in the spring. *Haploperla brevis* (Banks), a common eastern species, is 6–9 mm long, bright yellow, and has no anal lobe in the hind wing. The stoneflies belonging to the genus *Alloperla*, of which there are several eastern species, are green, average 8–15 mm, and have a small anal lobe in the hind wing.

Collecting and Preserving Plecoptera

During the warmer days in the fall, winter, and spring, adults of the winter species can be found resting on bridges, fence posts, and other objects near the streams in which the nymphs develop. Many species can be collected by sweeping the foliage along the banks of streams. Using a beating sheet is the preferred method of collecting adult stoneflies. Bridges are a favorite resting place for many species throughout the year. Many of the summer forms are attracted to lights. The nymphs can be found in streams, usually under stones or in the bottom debris.

Both adult and nymphal stoneflies should be preserved in alcohol. Pinned adults often shrink, with the result that some characters, particularly those of the genitalia and the gill remnants, are difficult to make out.

References

Baumann, R. W. 1987. Order Plecoptera. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 186–195. Dubuque, IA: Kendall/Hunt, 754 pp.

Baumann, R. W., A. R. Gaufin, and R. F. Surdick. 1977. The stoneflies (Plecoptera) of the Rocky Mountains. Mem. Amer. Entomol. Soc. 31, 208 pp.

Claassen, P. W. 1931. Plecoptera nymphs of America (north of Mexico). Thomas Say Foundation Publ. 3, 199 pp.

Frison, T. H. 1935. The stoneflies, or Plecoptera, of Illinois. Ill. Nat. Hist. Surv. Bull. 20(4):281–471.

Frison, T. H. 1942. Studies of North American Plecoptera, with special reference to the fauna of Illinois. Ill. Nat. Hist. Surv. Bull. 22(2):231–355.

Gaufin, A. R., A. V. Nebeker and J. Sessions. 1966. The stoneflies (Plecoptera) of Utah. Univ. Utah Biol. Ser. 14:9–89.

Harper, P. P. 1984. Plecoptera. In R. W. Merritt and K. W. Cummins (Eds.), An Introduction to the Aquatic Insects of North America, 2nd ed., pp. 182–230 Dubuque, IA: Kendall/Hunt.

Hitchcock, S. W. 1974. Guide to the insects of Connecticut. Part VII. The Plecoptera or stoneflies of Connecticut. Conn. State Geol. Nat. Hist. Surv. Bull. 107:1–262.

Illies, J. 1965. Phylogeny and zoogeography of the Plecoptera. Annu. Rev. Entomol. 10:117–140.

Jewett, S. G., Jr. 1956. Plecoptera. In R. L. Usinger (Ed.), Aquatic Insects of California, pp. 155–181. Berkeley: University of California Press.

Jewett, S. G., Jr. 1959. The stoneflies (Plecoptera) of the Pacific Northwest. Ore. State Monogr. No. 3, 95 pp.

Kondratieff, B. C., and R. F. Kirchner. 1987. Additions, taxonomic corrections, and faunal affinities of the stoneflies of Virginia, USA. Proc. Entomol. Soc. Wash. 89:24–30.

Needham, J. G., and P. W. Claassen. 1925. A monograph of the Plecoptera or stoneflies of America north of Mexico. Thomas Say Foundation Publ. 2, 397 pp.

Nelson, C. R., and R. W. Baumann. 1989. Systematics and distribution of the winter stonefly genus *Capnia* (Plecoptera: Capniidae) in North America. Gr. Basin Natur. 49:289–363.

Pennak, R. W. 1978. Fresh-Water Invertebrates of the United States, 2nd ed. New York: Wiley Interscience, 803 pp.

Ricker, W. E. 1952. Systematic studies in Plecoptera. Ind. Univ. Stud. Sci. Ser. 18:1–200.

Ricker, W. E. 1959. PlecopteraIn W. T. Edmondson (Ed.), Fresh-Water Biology, pp. 941–957. New York: Wiley.

Ross, H. H., and W. E. Ricker. 1971. The classification, evolution, and dispersal of the winter stonefly genus *Allocapnia*. Ill. Biol. Monogr. No. 43, 240 pp.

Stanger, J. A., and R. W. Baumann. 1993. A revision of the stonefly genus *Taenionema* (Plecoptera: Taeniopterygidae). Trans. Amer. Entomol. Soc. 119:171–229.

Stark, B. P., and C. R. Nelson. 1994. Systematics, phylogeny and zoogeography of genus *Yoraperla* (Plecoptera: Peltoperlidae). Entomol. Scand. 25:241–273.

Stark, B. P., K. W. Stewart, W. W. Szczytko, and R. W. Baumann. 1998. Common names of stoneflies (Plecoptera) from the United States and Canada. Ohio Biol. Surv. Notes 1:1–18.

Stark, B. P., S. W. Szczytko, and R. W. Baumann. 1986. North American stoneflies (Plecoptera): Systematics, distribution, and taxonomic references. Gr. Basin Nat. 46:383–397.

Stark, B. P., S. W. Szczytko, and C. R. Nelson. 1998. American stoneflies: A photographic guide to the Plecoptera. Columbus, OH: Caddis Press, 126 pp.

Stewart, K. W., and B. P. Stark. 1984. Nymphs of North American Perlodinae genera (Plecoptera: Perlodidae). Gr. Basin Nat. 44:373–415.

Stewart, K. W., and B. P. Stark. 1988. Nymphs of North American stonefly genera (Plecoptera). Thomas Say Foundation Publ. 12. 460 pp. (Reprinted in 1993 by University of North Texas Press.)

Surdick, R. F. 1985. Nearctic genera of Chloroperlinae (Plecoptera: Chloroperlidae). Ill. Biol. Monogr. 54:1–146.

Surdick, R. F., and K. C. Kim. 1976. Stoneflies (Plecoptera) of Pennsylvania, a synopsis. Bull. Penn. State Univ. Coll. Agr. 808:1–73.

Szczytko, S. W., and K. W. Stewart. 1979. The genus *Isoperla* (Plecoptera) of western North America; holomorphology and systematics, and a new stonefly genus *Cascadoperla*. Mem. Amer. Entomol. Soc. 32:1–120.

Unzicker, J. D., and V. H. McCaskill. 1982. Plecoptera. In A. R. Brigham and W. U. Brigham: Aquatic Insects and Oligochaetes of North and South Carolina. Mahomet, IL: Midwest Aquatic Enterprises, 837 pp.

Zwick, P. 1973. Insecta: Plecoptera, phylogenetisches System und Katalog. Das Tierreich 94:1–465 pp.

Zwick, P. 2000. Phylogenetic system and zoogeography of the Plecoptera. Annu. Rev. Entomol. 45:709–746.

17

Order Embiidina[1,2]

Web-Spinners

The web-spinners, perhaps more appropriately called "foot-spinners," are small, slender, chiefly tropical insects, represented by 11 species in the southern United States. The body of adult males is somewhat flattened, but that of females and young is cylindrical. Most species are about 10 mm in length. The antennae are filiform, ocelli are lacking, and the head is prognathous, with chewing mouthparts. Adult males do not eat, their mandibles being used mostly for chewing entry into a gallery and for grasping the female's head prior to copulation. The legs are short and stout; the tarsi have three segments; and the hind femora are greatly enlarged because of large tibial depressor muscles powering defensive reverse movement. The basal segment of the front tarsus is enlarged and contains silk glands. The silk is spun from a hollow, setalike ejector on the ventral surface of the basal and second tarsal segments that transport fluid silk from the numerous globular glands. The males of most species are winged, but some are wingless or have only vestigial wings. Both winged and wingless males may occur in the same species. The females are always wingless and neotenic. The wings are similar in size, shape, and somewhat reduced venation (Figure 17–1A). The venation is characterized by broadened, dead-end blood-sinus veins, which stiffen for flight by blood pressure. When not in use, the wings are very flexible and can fold forward to reduce the "barb effect" during predator-avoiding reverse movements. The abdomen, 10-segmented with rudiments of the eleventh, bears a pair of cerci. The cerci are two-segmented, but in adult males of some species the distal segment of the left cercus is absorbed into the basal one. The terminal appendages of the female are always symmetrical, but they are asymmetrical in the males of most species. Web-spinners undergo simple metamorphosis. One introduced Mediterranean species in the United States is parthenogenetic.

Web-spinners spend most of their lives in a labyrinth of silken galleries spun in leaf litter, under stones, in soil cracks, in bark crevices, and in epiphytic plants. Most other silk-producing insects use silk produced by modified rectal glands or by salivary glands opening near the mouth, but web-spinners produce the silk from glands in the front tarsi. All instars, even the first, can spin silk. Most species live in colonies made up of a parent female and her brood. Web-spinners often feign death when disturbed, but on occasion can move very rapidly, usually backward. The eggs are elongate-oval and are usually laid in a single-layered patch in the galleries. In most species the eggs are coated with a hardened paste of chewed habitat material or fecal pellets, which must reduce the chances of oviposition by egg parasitoid wasps. Females guard their eggs and early-stage nymphs. Web-spinners feed mostly on dead plant materials, which also constitute the substrate of their galleries. Embiids are easily cultured in tubes or jars containing habitat material, and this is the best method of obtaining adult males, which are usually required for identification to family. Determination is usually based on the form of the terminal abdominal structures (terminalia). Males of most species mature during a limited time each year, those of some species, especially *Oligotoma*, fly to light during warm, humid nights.

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[1] Embiidina: *embio*, lively.

[2] This chapter was written by Edward S. Ross, with minor editorial changes by the authors.

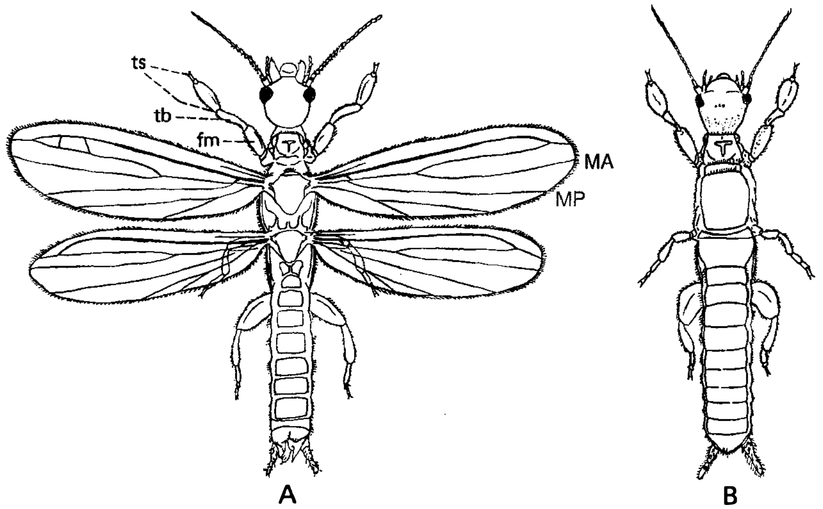

Figure 17–1 A web-spinner, *Oligotoma saundersii* (Westwood). A, winged male; B, wingless female. *fm*, femur; *tb*, tibia; *ts*, tarsus.

Key to the Families of Embiidina

1.	Adults and immatures with 2 bladderlike papillae on ventral surface of basal segment of hind tarsus (*Haploembia*)	Oligotomidae (in part)	p. 248
1′.	Adults and immatures with only 1 bladderlike papilla on ventral surface of hind tarsus	2	
2(1′).	Mandibles of adult males dentate apically; left cercus 2-segmented, inner surface of basal segment lacking peglike setae	3	
2′.	Mandibles of adult males not dentate apically; left cercus 1-segmented, inner surface of apex with a few peglike setae	**Anisembiidae**	p. 248
3(2).	MA forked	**Teratembiidae**	p. 248
3′.	MA not forked (Figure 17–1A)	Oligotomidae (in part)	p. 248

***Family* Anisembiidae:** The Anisembiidae are represented in the United States by three species: *Anisembia texana* (Melander) of the south central states, and *Dactylocerca rubra* (Ross) and *D. ashworthi* Ross of the Southwest. In some habitats, both winged and wingless males occur in colonies of *A. texana*. In humid regions, males are always alate, whereas in colder and arid regions males are always apterous.

***Family* Teratembiidae (Oligembiidae):** This family is represented in the southeastern United States by five species: *Oligembia hubbardi* (Hagen) of Florida, *O. melanura* Ross of Louisiana and Texas, *Diradius lobatus* (Ross) in the lower Rio Grande valley of Texas, *D. caribbeanus* (Ross) in the Florida Keys, and *D. vandykei* (Ross) of the Southeast.

***Family* Oligotomidae:** The Oligotomidae are represented in the United States by three introduced Old World species: *Oligotoma saundersii* (Westwood) of the southeastern states, *O. nigra* Hagen of the Southwest (extending as far east as San Antonio, Texas), and *Haploembia solieri* (Rambur) of the Southwest (extending as far north as southern Oregon). The last species is parthenogenetic, but a bisexual form has recently been introduced into central California.

Collecting and Preserving Embiidina

The males, which are generally more easily identified than the females, are often collected at lights, during and after the rainy season while the soil or bark is damp. None of the Anisembiidae fly to light, nor do those of melanic *Oligembia melanura*. Well-pigmented or melanic males apparently never disperse at night. Most individuals encountered in the colonies may be immature, but both sexes can be reared to maturity in jars, or large cotton-plugged tubes containing some dried grass and leaves that are kept somewhat moist.

Web-spinners, preferably adults, should be preserved in 70% alcohol. For detailed study, it may be desirable to clear the specimens in potassium hydroxide (KOH), and following proper procedures, to mount them on microscope slides (see Ross 1940, p. 634).

References

Ross, E. S. 1940. A revision of the Embioptera of North America. Ann. Entomol. Soc. Amer. 33:629–676.

Ross, E. S. 1944. A revision of the Embioptera of the New World. Proc. U.S. Natl. Mus. 94(3175):401–504.

Ross, E. S. 1970. Biosystematics of the Embioptera. Annu. Rev. Entomol. 15:157–171.

Ross, E. S. 1984. A synopsis of the Embiidina of the United States. Proc. Ent. Soc. Wash. 86:82–93.

Ross, E. S. 1987. Order Embiidina (Embioptera). In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 179–183. Dubuque, IA: Kendall/Hunt, 754 pp.

Ross, E. S. 2000. EMBIA, Contributions to the biosystematics of the insect order Embiidina. Parts 1 and 2. Occ. Papers California Academy of Sciences, No. 149; Part 1, 53 pp.; part 2, 36 pp.

Ross, E. S. 2001. EMBIA. Contributions to the biosystematics of the insect order Embiidina. Part 3. The Embiidae of the Americas (Order Embiidina). Occ. Papers California Academy of Sciences, No. 150, 86 pp.

18

Order Zoraptera[1]

Zorapterans, Angel Insects

The zorapterans are minute insects, 3 mm or less in length, and may be winged or wingless. The winged forms are generally dark, and the wingless forms are usually pale. The zorapterans are a little like termites in general appearance and are gregarious. The order was not discovered until 1913.

Winged and wingless forms occur in both sexes. The four wings are membranous, with very reduced venation and with the hind wings smaller than the front wings (Figure 18–1A). The wings of the adult are eventually shed, as in ants and termites, leaving stubs attached to the thorax. The antennae are moniliform and nine-segmented as adults. The wingless forms (Figure 18–1D) lack both compound eyes and ocelli, but the winged forms have compound eyes and three ocelli. The tarsi are two-segmented, and each tarsus bears two claws. The cerci are short and unsegmented and terminate in a long bristle. The abdomen is short, oval, and 10-segmented. The mouthparts are of the chewing type, and the metamorphosis is simple. Apparently there are four juvenile instars in the common species in North America.

Some wingless males of certain species have a cephalic fontanelle. This is true of *Usazoros hubbardi* (Caudell). The gland may secrete a pheromone that helps keep the largely blind gregarious assemblage together in their dark habitat. Delamare Deboutteville (1956) considered the zorapteran fontanelle as probably homologous with that of termites.

The order Zoraptera contains a single family, the Zorotypidae, and seven genera. In 1978, New listed 28 described species of zorapterans, and since then two more species have been found in southeast Tibet. Three species occur in the United States. *Usazoros hubbardi* has been taken in a number of localities in 33 states in the central, eastern, and southern United States, from Maryland and southern Pennsylvania westward to southern Iowa and southward to Florida and Texas; *Zorotypus swezeyi* Caudell is known from Hawaii; *Floridazoros snyderi* (Caudell) occurs in Florida and Jamaica. *Usazoros hubbardi* is commonly found under slabs of wood buried in piles of old sawdust. Colonies are also found under bark and in rotting logs. The principal food of zorapterans appears to be fungal spores, but they are known to eat small dead arthropods.

Collecting and Preserving Zoraptera

Zorapterans are to be looked for in the habitats indicated previously and are generally collected by sifting debris or by means of a Berlese funnel (Figure 35–5). Where zorapterans are abundant, an aspirator is very useful. They should be preserved in 70% alcohol and may be mounted on microscope slides for detailed study.

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[1] Zoraptera: *zor*, pure; *aptera*, wingless. Only wingless individuals were known when this order was described, and entomologists thought the wingless condition was a distinctive feature of the order.

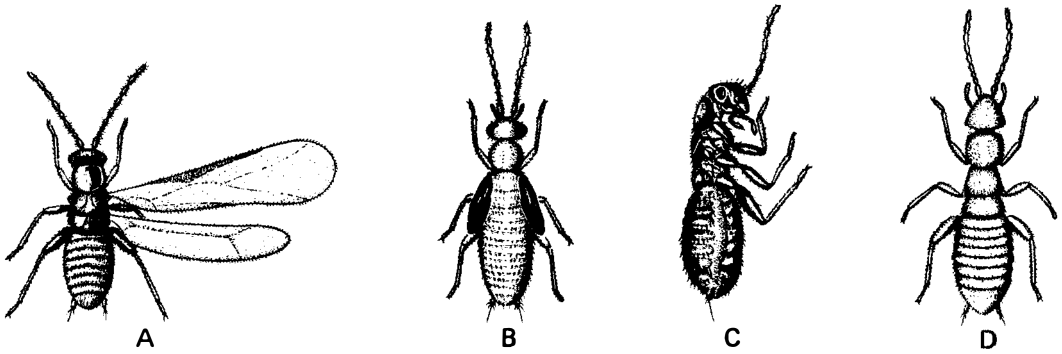


Figure 18–1 *Usazoros hubbardi* (Caudell). A, winged adult; B, nymph of winged form; C, dealated winged adult, lateral view; D, wingless adult. (Courtesy of Caudell.)

References

Caudell, A. N. 1918. *Zorotypus hubbardi*, a new species of the order Zoraptera from the United States. Can. Entomol. 50:375–381.

Caudell, A. N. 1920. Zoraptera not an apterous order. Proc. Entomol. Soc. Wash. 22:84–97.

Caudell, A. N. 1927. *Zorotypus longiceratus*, a new species of Zoraptera from Jamaica. Proc. Entomol. Soc. Wash. 29:144–145.

Delamare Deboutteville, C. 1956. Zoraptera. In S. L. Tuxen (Ed.), Taxonomist's Glossary of Genitalia in Insects, pp. 38–41. Copenhagen: Munksgaard.

Gurney, A. B. 1938. A synopsis of the order Zoraptera, with notes on the biology of *Zorotypus hubbardi* Caudell. Proc. Entomol. Soc. Wash. 40:57–87.

Gurney, A. B. 1959. New distribution records for *Zorotypus hubbardi* Caudell (Zoraptera). Proc. Entomol. Soc. Wash. 61:183–184.

Gurney, A. B. 1974. Class Insecta, Order Zoraptera. In W. G. H. Coaton (Ed.), Status of the Taxonomy of the Hexapoda of Southern Africa. RSA Dept. Agr. Tech. Serv., Entomol. Mem. 38:32–34.

Kukalová-Peck, J., and S. B. Peck. 1993. Zoraptera wing structures: Evidence for new genera and relationship with the blattoid orders (Insecta: Blattoneoptera). Syst. Entomol. 18:333–350.

New, T. R. 1978. Notes on Neotropical Zoraptera, with descriptions of two new species. Syst. Entomol. 3:361–370.

Riegel, G. T. 1963. The distribution of *Zorotypus hubbardi* (Zoraptera). Ann. Entomol. Soc. Amer. 56:744–747.

Riegel, G. T. 1969. More Zoraptera records. Proc. North Central Branch, Entomol. Soc. Amer. 23(2):125–126.

Riegel, G. T. 1987. Order Zoraptera. In F. W. Stehr (Ed.), Immature Insects, pp. 184–185. Dubuque, IA: Kendall/Hunt.

Riegel, G. T., and S. J. Eytalis. 1974. Life history studies on Zoraptera. Proc. North Central Branch, Entomol. Soc. Amer. 29:106–107.

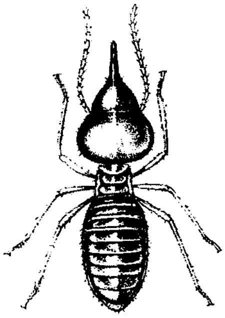
Riegel, G. T., and M. B. Ferguson. 1960. New state records of Zoraptera. Entomol. News 71(8):213–216.

St. Amand, W. 1954. Records of the order Zoraptera from South Carolina. Entomol. News 65(5):131.

19

Order Isoptera[1,2]

Termites



Termites are medium-sized, cellulose-eating social insects making up the order Isoptera, a relatively small group of insects, consisting of approximately 1900 species worldwide. They live in highly organized and integrated societies, or colonies, with the individuals differentiated morphologically into distinct forms or castes—reproductives, workers, and soldiers—that perform different biological functions. The four wings (present only in the reproductive caste) are membranous. The front and hind wings are almost equal in size (Figure 19–1), hence the name Isoptera. The antennae are moniliform or filiform. The mouthparts of the workers and reproductives are of the chewing type. The metamorphosis is simple. The nymphs have the potential to develop into any one of the castes. Experiments have shown that hormones and inhibitory pheromones secreted by the reproductives and soldiers regulate caste differentiation.

Although termites are popularly referred to as "white ants," they are not ants, nor are they closely related to ants, which are grouped with bees and wasps in the Hymenoptera, whose social system has evolved independently of that in the Isoptera. Termites are most closely related to the cockroaches and mantids (Thorne and Carpenter 1992, Wheeler et al. 2001). The primitive living species *Mastotermes darwiniensis* Froggatt from Australia has some similarities with some cockroaches, such as the folded anal lobe in the hind wing and an egg mass resembling the oothecae of cockroaches and mantids. However, the *Mastotermes* egg mass differs in structural details from the ootheca and is probably more similar to egg pods of other Orthoptera. The relationship to the monophyletic group of Blattodea + Mantodea suggests that termites evolved in the late Permian, approximately 200 million years ago (although the known fossil termites date only from the Cretaceous, about 120 million years ago). The termite society is therefore the oldest.

There are many important differences between termites and ants. Termites are soft-bodied and usually light-colored, whereas ants are hard-bodied and usually dark. The antennae in termites are not elbowed as in ants. The front and hind wings of termites are nearly equal in size and are held flat over the abdomen at rest, whereas in ants the hind wings are smaller than the fore wings and the wings at rest are usually held above the body. In termites, the wings, when shed, break along a suture, leaving only the wing base, or "scale," attached to the thorax. The abdomen in termites is broadly joined to the thorax, whereas in ants it is constricted at the base, forming the characteristic hymenopteran petiole, or "waist." The sterile castes

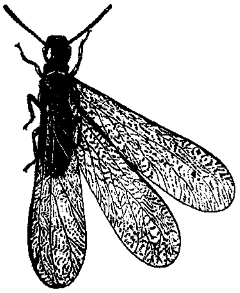


Figure 19–1 A winged termite. (Courtesy of USDA.)

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[1] Isoptera: *iso*, equal; *ptera*, wings.

[2] This chapter was edited by Kumar Krishna.

(workers and soldiers) in termites are made up of both sexes, and reproductives and sterile castes develop from fertilized eggs. In ants, the sterile castes are made up of females only, and all females, sterile and reproductive, develop from fertilized eggs, whereas the reproductive males develop from unfertilized eggs.

Termite Castes

The reproductive function in the termite society is carried out by the primary reproductives, the king and queen—most commonly one pair to a colony—which develop from fully winged (macropterous) adults (Figure 19–2A). They are heavily sclerotized and have compound eyes. The king is generally small, but in many species the queen develops an enlarged abdomen as a result of her increasing egg-laying capacity, and in some tropical species she can reach a size as great as 11 cm (compared with 1–2 cm for the king). The winged reproductives from which the king and queen develop are produced in large numbers seasonally. They leave the colony in a swarming or colonizing flight, shed their wings along a suture, and, as individual pairs, seek a nesting site, mate, and establish new colonies. Some species have one emergence a year; others have many. In the most common eastern species, *Reticulitermes flavipes* (Kollar), emergence occurs in the spring; in some western species, it occurs in late summer, whereas other species also swarm between January and April.

In the initial stages of colony foundation, the reproductives feed the young and tend to the nest, but young nymphs and workers soon take over these household duties.

If it happens that the king and queen die or part of the colony is separated from the parent colony, supplementary reproductives develop within the nest and take over the function of the king and queen. The supplementary reproductives are slightly sclerotized and pigmented, with short wing pads (brachypterous) or no wing pads (apterous) and reduced compound eyes. They develop from nymphs and achieve sexual maturity without reaching the fully winged adult stages and without leaving the nest.

The worker and soldier castes, made up of both sexes, are sterile, wingless, in most species blind, and in some species polymorphic, that is, of two or more distinct sizes (Figure 19–2C,D).

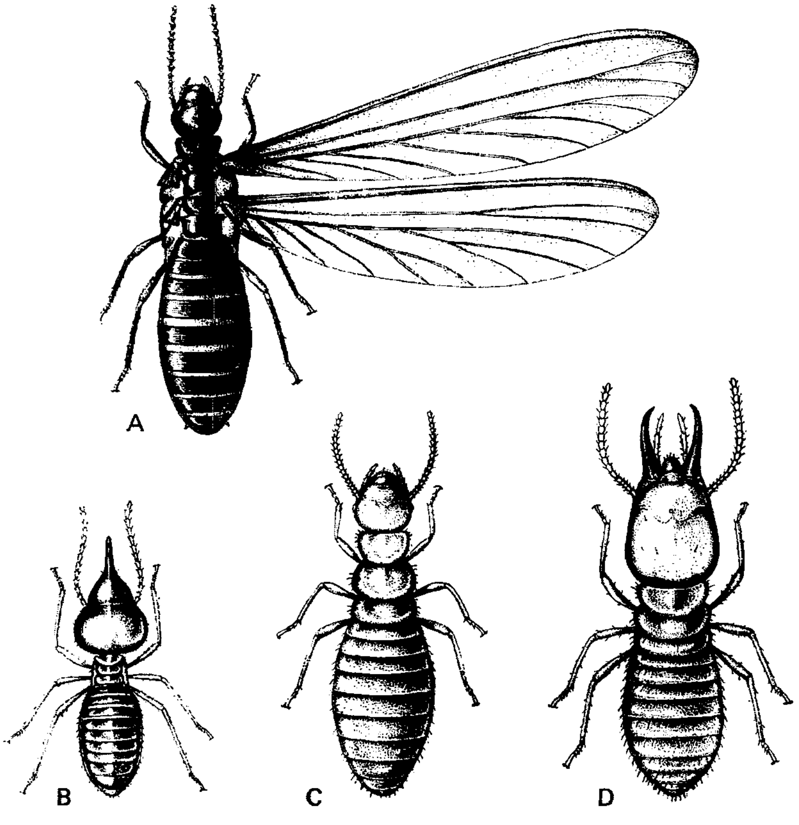

Figure 19–2 Castes of termites. A, sexual winged adult, *Amitermes wheeleri* (Desneux), 10× (Termitidae); B, nasute soldier of *Tenuirostritermes tenuirostris* (Desneux), 15× (Termitidae); C, worker, and D, soldier of *Prorhinotermes simplex* (Hagen), 10× (Rhinotermitidae). (Courtesy of Banks and Snyder and the U.S. National Museum.)

The workers are usually the most numerous individuals in a colony. They are pale and soft-bodied, with mouthparts adapted for chewing. They perform most of the work of the colony: nest building and repair, foraging, and feeding and grooming the other members of the colony. Because of its feeding function, the worker caste causes the widespread destruction for which termites are notorious. In the primitive families, a true worker caste is absent and its functions are carried out by wingless nymphs called pseudergates, which may molt from time to time without change in size.

The soldier has a large, dark, elongated, highly sclerotized head, adapted in various ways for defense. In the soldiers of most species, the mandibles are long, powerful, hooked, and modified to operate with a scissorlike action to behead, dismember, or lacerate enemies or predators (usually ants). In the soldiers of some genera, such as *Cryptotermes*, the head is short and truncated in front and is used in defense to plug entrance holes in the nest.

The mechanical means of defense are sometimes supplemented or displaced by chemical means, in which a sticky and toxic fluid is secreted by the frontal gland and ejected through an opening onto the enemy. In *Coptotermes* and *Rhinotermes*, the gland occupies a large portion of the head. In the subfamily Nasutitermitinae, the mechanism of defense is exclusively chemical: the mandibles are reduced, the frontal gland is greatly enlarged, and the head has developed a snout, or nasus (Figure 19–2B) through which a sticky, repellent secretion is squirted at the enemy.

In a few genera, such as *Anoplotermes*, the soldier caste is absent, and the nymphs and workers defend the colony.

Habits of Termites

Termites frequently groom each other with their mouthparts, probably as a result of the attraction of secretions that are usually available on the body. The food of termites consists of the cast skins and feces of other individuals, dead individuals, and plant materials such as wood and wood products.

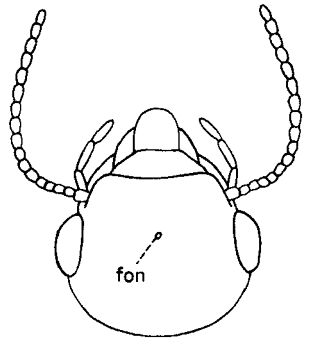

Figure 19–3 Head of *Prorhinotermes*, dorsal view, showing fontanelle (*fon*). (Modified from Banks and Synder.)

Some termites live in moist subterranean habitats, and others live in dry habitats aboveground. The subterranean forms normally live in wood buried beneath or in contact with the soil. They may enter wood remote from the soil, but must maintain a passageway or connecting gallery to the soil, from which they obtain moisture. Some species construct earthen tubes between the soil and wood aboveground. These tubes are made of dirt mixed with a secretion from a pore on the front of the head (the fontanelle; Figure 19–3, fon). The nests may be entirely subterranean, or they may protrude above the surface: Some tropical species have nests (termitaria) 9 meters high. The drywood termites, which live aboveground (without contact with the ground), live in posts, stumps, trees, and buildings constructed of wood. Their chief source of moisture is metabolic water (water resulting from the oxidation of food).

The cellulose in a termite's food is digested by myriads of flagellate protists living in the termite's digestive tract. A termite from which these flagellates have been removed will continue to feed, but it will eventually starve to death because its food is not digested. This association is an excellent example of symbiosis, or mutualism. Some termites harbor bacteria rather than flagellates. Termites engage in a unique form of anal liquid exchange (trophallaxis), and this is how intestinal microorganisms are transmitted from one individual to another.

Key to the Families of Isoptera (Winged Adults)

1.	Fontanelle usually present (Figure 19–3, fon); wings with only 2 heavy veins in anterior part of wing beyond scale, R usually without anterior branches (Figure 19–4A)	2
1′.	Fontanelle absent; wings with 3 or more heavy veins in anterior part of wing beyond scale, R with 1 or more anterior branches (Figure 19–4B)	3

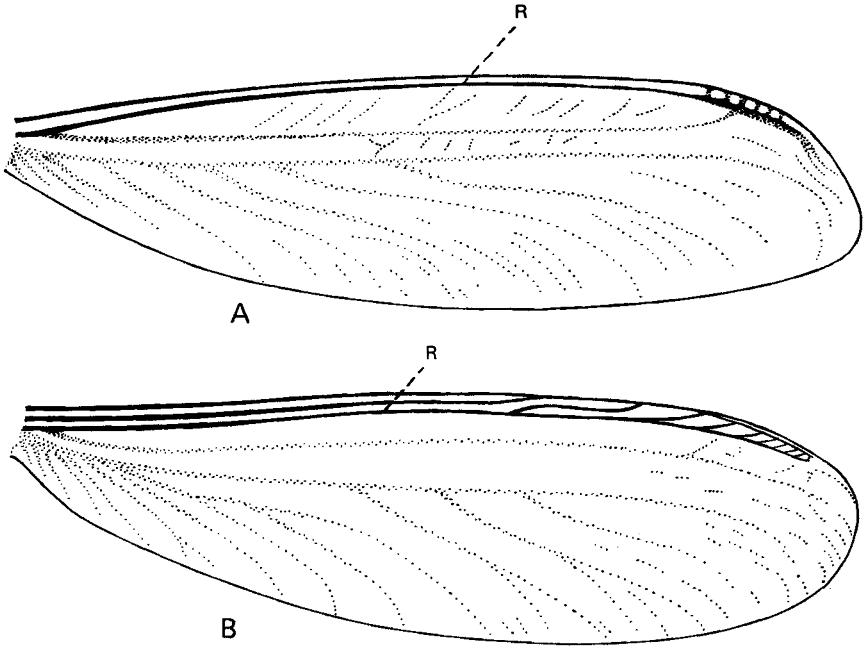

Figure 19–4 Wings of termites. A, Rhinotermitidae; B, Kalotermitidae.

2(1).	Scale of front wing longer than pronotum; pronotum flat; cerci 2-segmented; widely distributed	Rhinotermitidae	p. 256
2′.	Scale of front wing shorter than pronotum; pronotum saddle-shaped; cerci 1- or 2-segmented; southwestern United States	Termitidae	p. 257
3(1′).	Ocelli present; shaft of tibiae without spines; antennae usually with fewer than 21 segments; cerci short, 2-segmented; Florida and western United States	Kalotermitidae	p. 256
3′.	Ocelli absent; shaft of tibiae usually with spines; antennae usually with more than 21 segments; cerci long, 4-segmented; western United States, southern British Columbia, and Queen Charlotte Island	Termopsidae	p. 256

Key to the Families of Isoptera (Soldiers)

1.	Mandibles vestigial, the head produced anteriorly into a long, noselike projection (nasute soldiers; Figure 19–2B)	Termitidae	p. 257
1′.	Mandibles normal, head not as in preceding entry	2	
2(1′).	Head longer than broad (Figure 19–2D); mandibles with or without prominent marginal teeth	3	
2′.	Head short, hollowed out; mandibles without marginal teeth; southern United States (powderpost termites)	Kalotermitidae	p. 256
3(2).	Mandibles with one or more prominent marginal teeth; southern and western United States	4	
3′.	Mandibles without marginal teeth (Figure 19–2D); widely distributed	Rhinotermitidae	p. 256

4(3).	Mandibles with only 1 prominent marginal tooth; head narrowed anteriorly	**Termitidae**	p. 257
4′.	Mandibles with more than 1 prominent marginal tooth; head not narrowed anteriorly	5	
5(4′).	Third antennal segment modified; hind femora swollen	**Kalotermitidae**	p. 256
5′.	Third antennal segment not modified; hind femora variable	6	
6(5′).	Hind femora swollen; antennae with at least 23 segments; shaft of tibiae with spines	**Termopsidae**	p. 256
6′.	Hind femora not, or only slightly, swollen; antennae with fewer than 23 segments; shaft of tibiae without spines	Kalotermitidae	p. 256

***Family* Kalotermitidae:** This family is represented in the United States by 17 species and includes drywood, dampwood, and powderpost termites. These termites have no worker caste, and the young of the other castes perform the work of the colony. The kalotermitids lack a fontanelle and do not construct earthen tubes.

The drywood termites (*Incisitermes*, *Pterotermes*, and *Marginitermes*) attack dry, sound wood and do not have a ground contact. Most infestations are in the structure of buildings, but furniture, utility poles, and piled lumber may also be attacked. Adults are cylindrical and about 13 mm long, and the reproductives are pale brown. *Incisitermes minor* (Hagen) and *Marginitermes hubbardi* (Banks) are important species in the southwestern states.

The dampwood termites in this family (*Neotermes* and *Paraneotermes*) attack moist, dead wood, tree roots, and the like. They occur in Florida and the western United States.

The powderpost termites (*Cryptotermes* and *Calcaritermes*) usually attack dry wood (without a soil contact) and reduce it to powder. They occur in the southern United States. *Cryptotermes brevis* (Walker) is an introduced species in the United States. It occurs along the Gulf Coast near Tampa and New Orleans and has been found as far north as Tennessee. It was probably introduced in furniture. It attacks furniture, books, stationery, dry goods, and building timbers. It frequently does a great deal of damage. It is found in buildings, never outdoors. Where it is found, its colonies are numerous but small.

***Family* Termopsidae—Dampwood Termites:** This group includes three species of *Zootermopsis*, which occur along the Pacific Coast north to southern British Columbia. The adults are 13 mm or more in length, are somewhat flattened, and lack a fontanelle. There is no worker caste. These termites attack dead wood, and although they do not need a ground contact, some moisture in the wood is required. They generally occur in dead, damp, rotting logs, but frequently damage buildings, utility poles, and lumber, particularly in coastal regions where there is considerable fog.

The most common species in this group are *Z. nevadensis* Banks and *Z. angusticollis* (Hagen). *Zootermopsis nevadensis* is a little over 13 mm long and lives in relatively dry habitats (especially dead tree trunks). The wingless forms are pale with a darker head, and the winged forms are dark brown with the head chestnut or orange. *Zootermopsis angusticollis* is larger (about 18 mm long) and generally occurs in damp, dead logs. Adults are pale with a brown head.

***Family* Rhinotermitidae:** This group is represented in the United States by nine species (with one species extending northward into Canada) and includes the subterranean termites (*Reticulitermes* and *Heterotermes*) and the dampwood termites in the genus *Prorhinotermes* (Figure 19–2C,D). *Reticulitermes* is widely distributed, *Heterotermes* is found only in the western and southern United States, and the dampwood termites occur only in Florida. These termites are small (adults are about 6–8 mm long). Wingless forms are very pale (soldiers have a pale brown head), and winged forms are black. There is a fontanelle on the front of the head (Figure 19–3, fon). The members of this group always maintain contact with the soil. They often construct earthen tubes to wood not in contact with the soil. The eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Figure 19–5), is probably the most destructive species in the order and is the only termite in the Northeast.

The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, a native of mainland China and Taiwan, and one of the most destructive species in the world, has become established in many areas of the globe, including Japan, Guam, Hawaii, and South Africa. It was first introduced into the continental United States in 1965 in Houston, Texas, and has since spread to many


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Figure 19–5 A group of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar); note the soldier in the right central portion of the picture.

southern states: Alabama, Louisiana, Mississippi, Georgia, Florida, Tennessee and North and South Carolina. It attacks living trees as well as old tree stumps, poles, and other wood structures. The nest is underground or in wood. A colony may take several years to mature, at which time it contains several million individuals. The soldier of this species can be recognized by its oval head, with a large fontanelle opening in the front margin, which exudes a whitish, sticky substance.

Family **Termitidae:** This group is represented in the United States by 15 species, most of them in the Southwest. It includes the soldierless termites (*Anoplotermes*), the desert termites (*Amitermes* and *Gnathamitermes*), and the nasutiform termites (*Tenuirostritermes*). The soldierless termites burrow under logs or cow dung and are not of economic importance. The desert termites are subterranean and occasionally damage the wood of buildings, poles, and fence posts. The nasutiform termites normally attack desert shrubs or other objects on the ground and maintain a ground contact.

Economic Importance of Termites

Termites hold two positions from the economic point of view. On the one hand, they may be very destructive, because they feed on and often destroy various structures or materials that people use: wooden portions of buildings, furniture, books, utility poles, fence posts, many fabrics, and the like (Figure 19–6). Worldwide they account for a high amount of atmospheric

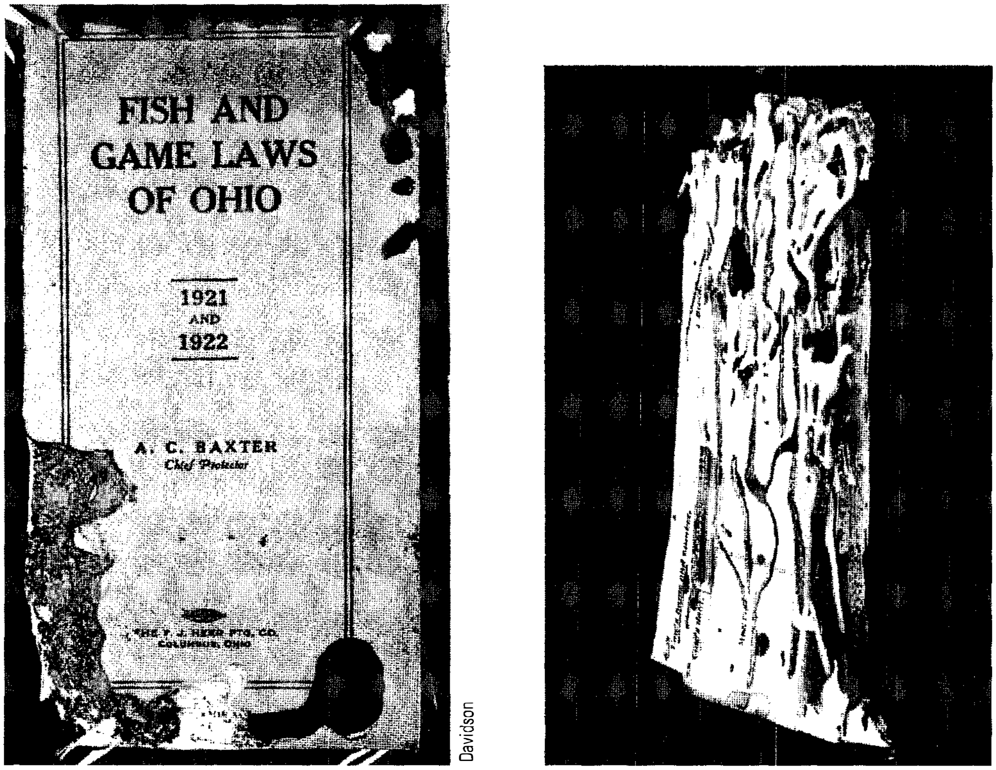

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Figure 19–6 Termite damage.

methane. On the other hand, they help convert dead trees and other plant products to substances that plants can use.

Reticulitermes flavipes is the common termite throughout the eastern United States. This species occurs in buried wood, fallen trees, and logs. It must maintain a ground connection to obtain moisture. It cannot initiate a new colony in the wood in a house; the nest in the soil must be established first. Once the soil nest is established, these termites may enter buildings from the soil in one of five ways: (1) through timbers that are in direct contact with the soil, (2) via openings in rough stone foundations, (3) through openings or cracks in concrete-block foundations, (4) through expansion joints or cracks in concrete floors, or (5) by means of earthen tubes constructed over foundations or in hidden cracks and crevices in masonry.

Infestations of the subterranean termite in a building may be recognized by the swarming of the reproductives in the spring in or about the building, by mud protruding from cracks between boards or beams or along basement joists, by the earthen tubes extending from the soil to the wood, or by the hollowness of the wood in which the insects have been tunneling. You can easily push a knife blade into a timber hollowed out by termites, and such wood readily breaks apart.

Subterranean termites in buildings are controlled by two general methods: by properly constructing the buildings to render them termite proof, and by using chemicals. The former involves construction in which no wood is in contact with the ground and in which the termites cannot reach the wooden part of the building through outside steps, through sills, or through the foundation. Control by chemicals involves their application to the wood or to the soil. Utility poles and fence posts, which must be in contact with the ground, may be rendered termite proof by chemical treatment.

The best method of eliminating drywood termites is by chemical fumigation. For such termites in buildings a large tent of plastic or other impervious material is placed over the entire building. The fumigant, usually sulfuryl fluoride, methyl bromide, or a combination of methyl bromide and carbon dioxide, is then pumped into the building. This is a rather expensive procedure. Drywood termites may also be eliminated by drilling holes in infested timbers, forcing a small amount of a poison dust into the holes, and then plugging up the holes. Termites constantly groom one another, and once a few individuals get this dust on themselves, the other individuals of the colony will eventually obtain it and be killed. Termite baits are now used to control subterranean termites.

Collecting and Preserving Isoptera

Termites can be found by turning over dead logs or by digging into dead stumps. They can be collected with forceps or a moistened brush, or they can be shaken out of infested timbers onto a paper. Preserve termites in 70 to 80% alcohol. Most individuals are very soft-bodied and shrivel or become distorted if mounted on pins or points. It is often necessary to mount these insects on microscope slides for detailed study.

References

Abe, T., D. E. Bignell, and M. Higashi (Eds.). 2000. Termites: Evolution, Sociality, Symbioses, Ecology. Dordrecht: Kluwer Academic, 488 pp.

Constantino, R. 1998. Catalog of the living termites of the New World (Insecta: Isoptera). Arquivos de Zoologia (São Paulo) 35(2):135–231.

Ebeling, W. 1968. Termites: Identification, biology, and control of termites attacking buildings. Calif. Agr. Expt. Sta. Extension Service Manual No. 38, 68 pp.

Ebeling, W. 1975. Urban Entomology. Berkeley: University of California Press, 695 pp.

Ernst, E., and R. L. Araujo. 1986. A Bibliography of Termite Literature, 1966–1978. Chichester, UK: Wiley, 903 pp.

Forschler, B. T. 1999. Part II. Subterranean termite biology in relation to prevention and removal of structural infestation. In National Pest Control Association (Ed.), NPCA Research Report on Subterranean Termites, pp. 31–52. Dunn Loring, VA: National Pest Control Association, 57 pp.

Krishna, K. 1961. A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). Bull. Amer. Mus. Nat. Hist. 122(4):307–408.

Krishna, K. 1966. A key to eight termite genera. Coop. Econ. Insect Rep. (USDA) 16(47):1091–1098.

Krishna, K, and F. M. Weesner (Eds.). 1969, 1970. Biology of termites. 2 vols. New York: Academic Press, vol. 1, 615 pp; vol. 2, 658 pp.

Miller, E. M. 1949. A Handbook of Florida Termites. Coral Gables, FL: University of Miami Press, 30 pp.

Skaife, S. H. 1961. Dwellers in Darkness. New York: Doubleday, 180 pp.

Snyder, T. E. 1935. Our Enemy the Termite. Ithaca, NY: Comstock, 196 pp.

Snyder, T. E. 1949. Catalogue of the termites (Isoptera) of the world. Smithson. Misc. Coll. 112(3953), 490 pp.

Snyder, T. E. 1954. Order Isoptera—The Termites of the United States and Canada. New York: National Pest Control Association, 64 pp.

Snyder, T. E. 1956. Annotated subject-heading bibliography of termites, 1350 B.C. to A.D. 1954. Smithson. Misc. Coll. 130(4258), 305 pp.

Snyder, T. E. 1961. Supplement to the annotated subject-heading bibliography of termites, 1955 to 1960. Smithson. Misc. Coll. 143(3), 137 pp.

Snyder, T. E. 1968. Second supplement to the annotated subject-heading bibliography of termites, 1961–1965. Smithson. Misc. Coll. 152, 188 pp.

Tamashiro, M., and N.- Y Su (Eds.). 1987. Biology and control of the Formosan subterranean termite: Proc. International symposium on the Formosan subterranean termite. 67th Meeting, Pacific Branch, Entomological Society of America, Honolulu, Hawaii, 1985. Honolulu: College of Tropical Agriculture and Human Resources, University of Hawaii, 61 pp.

Thorne, B. L. 1999. Part I. Biology of subterranean termites of the genus *Reticulitermes*. In National Pest Control Association (Ed.), NPCA Research Report on Subterranean Termites, pp. 1–30. Dunn Loring, VA: National Pest Control Association, 57 pp.

Thorne, B. L. and J. M. Carpenter. 1992. Phylogeny of the Dictyoptera. Syst. Entomol. 17:253–268.

Weesner, F. M. 1960. Evolution and biology of the termites. Annu. Rev. Entomol. 5:153–170.

Weesner, F. M. 1965. The Termites of the United States. A Handbook. Elizabeth, NJ: National Pest Control Association, 71 pp.

Weesner, F. M. 1987. Order Isoptera. In F. W. Stehr (Ed.), Immature Insects, pp. 132–139. Dubuque, IA: Kendall/Hunt.

Wheeler, W. C., M. Whiting, Q. D. Wheeler, and J. M. Carpenter. 2001. The phylogeny of the extant hexapod orders. Cladistics 17:113–169.

20

Order Mantodea[1,2]

Mantids

Mantids are large, elongate, rather slow-moving insects that are striking in appearance because of their peculiarly modified front legs (Figure 20–1). The prothorax is greatly lengthened and movably attached to the pterothorax; the front coxae are very long and mobile; and the front femora and tibiae are armed with strong spines and fitted for grasping prey. The head is freely movable. Mantids are the only insects that can "look over their shoulders." These insects are highly predaceous and feed on a variety of insects (including other mantids). They usually lie in wait for their prey with the front legs in an upraised position. This position has given rise to the common names "praying mantis" and "soothsayer" that are often applied to these insects.

Mantids overwinter in the egg stage, and the eggs are deposited on twigs or grass stems in a Styrofoam-like egg case or ootheca secreted by the female. Each egg case may contain 200 or more eggs. If brought into the house and kept warm, the eggs will hatch in late winter or early spring, and the nymphs, unless supplied with food, will eat each other until one, large nymph remains.

There are more than 1500 species in eight families of mantids in the world, most of which are tropical. The United States and Canada have only 17 species, all except one belonging to the family Mantidae. The Carolina mantis, *Stagmomantis carolina* (Johannson), which is about 50 mm in length (Figure 20–1), is the most common of several species of mantids occurring in the southern states. The large mantis (75–100 mm in length) that is locally common in the northern states is an introduced species, the Chinese mantis, *Tenodera aridifolia* (Stoll). This species was introduced in the vicinity of Philadelphia about 75 years ago and has since become rather widely distributed through the transportation of egg masses. Another species, *T. angustipennis* Saussure, the narrow-winged mantis, was

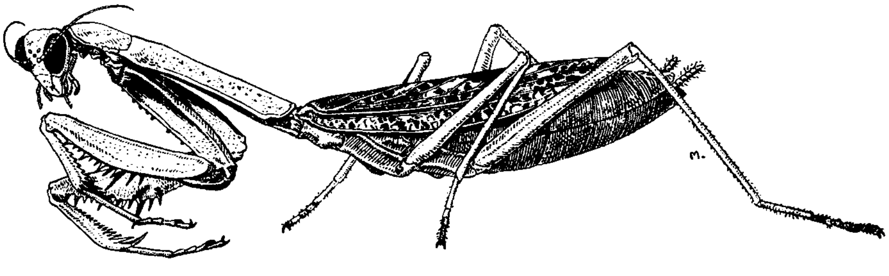

Figure 20–1 The Carolina mantid, *Stagomantis carolina* (Johansen). (Courtesy of Hebard and the Illinois Natural History Survey.)

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[1] Mantodea, from the Greek, meaning a soothsayer or a kind of grasshopper.

[2] This chapter was edited by David A. Nickle.

introduced from Asia. The European mantis, *Mantis religiosa* L., a pale-green insect about 50 mm in length, was introduced in the vicinity of Rochester, New York, about 75 years ago and now occurs throughout most of the eastern states.

The family Mantoididae has only one member in the United States, *Mantoidea maya* Saussura and Zehntner. It is small (length 15–17 mm) with the pronotum about as wide as long. It is found in southern Florida and Yucatán, Mexico.

Key to the Families and Subfamilies of Mantodea

1.	Pronotum quadrate or only slightly longer than wide; small species found only in south Florida	Mantoididae (*Mantoidea*, 1 sp.)
1′.	Pronotum distinctly longer than wide (Mantidae)	2
2(1′).	Fore femur with deep pit or groove between first and second spines on outer ventral margin to receive apical ventral claw of fore tibia	Liturgusinae (*Gonatista*, 1 sp.)
2′.	Fore femur lacking deep pit or groove between first and second spines on outer ventral margin	3
3(2′).	Outer ventral margin of fore femur with 5–7 spines; antenna basally broad, flattened	Photinae (*Brunneria*, 1 sp.)
3′.	Outer ventral margin of fore femur usually with 4 spines; antenna thin, filamentous	4
4(3′).	Fore tibia armed dorsoapically with 1–2 spines; long slender species	Oligonychinae (*Oligonicella*, 2 spp., *Thesprotia*, 1 sp.)
4′.	Fore tibia unarmed dorsoapically; more robust species	5
5(4′).	Small species, less than 35 mm long; eyes dorsally pointed (*Yersiniops*, 2 spp.) or costal margin of tegmen with dense coat of fine cilia (*Litaneutra*, 1 sp.)	Amelinae
5′.	Larger species, greater than 40 mm long; eyes globose, with costal margin of tegmen glabrous	Mantinae (*Pseudovates*, 1 sp.; *Iris*, 1 sp., *Mantis*, 1 sp.; *Tenodera*, 2 spp., *Stagmomantis*, 5 spp.)

The female mantid usually eats the male immediately after or actually during mating. No males are known for *Brunneria borealis* Scudder, a fairly common species in the South and Southwest.

Mantids are highly touted as biological control agents, and you can buy them to place in gardens to help control pest insects. This practice is not recommended because the mantids cannot possibly keep up with populations of damaging insects. In addition, mantids do not discriminate between destructive and useful insects and sometimes become a pest themselves, especially around beehives, where they may have a real feast of honey bees going to and from the hive.

Collecting and Preserving Mantodea

Mantids are relatively large and slow-moving and, once found, are fairly easy to collect. The best time for collecting the adults of most species is from midsummer to late fall. The egg masses are large and fairly conspicuous, especially on the bare twigs of trees during the winter. Pin adults through the right tegmen, in about the middle of the body (from front to rear). If the specimen is very soft-bodied, support the body by a piece of cardboard or by pins; otherwise, it will sag at either end.

References

Blatchley, W. S. 1920. Orthoptera of Northeastern America. Indianapolis: Nature, 785 pp.

Gurney, A. B. 1951. Praying mantids of the United States. Smithson. Inst. Rep. 1950:339–362.

Hebard, M. 1934. The Dermaptera and Orthoptera of Illinois. Ill. Nat. Hist. Surv. Bull. 20:125–179.

Helfer, J. R. 1987. How to Know the Grasshoppers, Cockroaches, and Their Allies, 2nd ed. New York: Dover Publications, 363 pp.

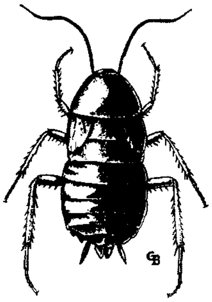
Nickle, D. A. 1987. Order Mantodea. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 140–142. Dubuque, IA: Kendall/Hunt, 754 pp.

Vickery, V. R., and D. K. McE. Kevan. 1985. The Grasshoppers, Crickets, and Related Insects of Canada and Adjacent Regions: Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera. The Insects and Arachnids of Canada, Part 14. Ottawa: Canadian Government Publishing Centre, 918 pp.

21

Order Blattodea[1,2]

Cockroaches



Cockroaches are cursorial insects with 5-segmented tarsi and none of the legs modified for digging or grasping. They run very fast, as anyone who attempts to step on one soon discovers. The body is oval and flattened, and the head is concealed from above by the pronotum. Tympana and stridulating organs usually are absent. Wings are generally present, although in some species they are much reduced. The females of many species have shorter wings than the males. The cerci are one- to many-segmented and usually fairly long; the antennae are long and filiform. These insects are rather generalized feeders. The eggs are enclosed in capsules or oothecae, which may be deposited immediately after they are formed, carried about on the end of the abdomen of the female until the eggs hatch, or carried internally in a uterus or brood pouch for the full gestation period.

Cockroaches are primarily tropical insects, and most North American species occur in the southern part of the United States. Some tropical species are occasionally brought into the North in shipments of bananas or other tropical fruits. The most commonly encountered cockroaches in the North are those that invade houses, where they are often serious pests. None is known to be a specific vector of disease, but they feed on all sorts of things in a house. They contaminate food, they have an unpleasant odor, and their presence is often very annoying.

Classification of the Blattodea

There is much difference of opinion regarding the classification of cockroaches. The 40-odd major groups are variously treated as tribes, subfamilies, or families by different authorities. We generally follow here the classification of McKittrick (1964), who groups the 50 or so North American species in five families. A synopsis of the North American Blattodea, as treated in this book, is given here. The groups marked with an asterisk (*) are relatively rare or are unlikely to be taken by a general collector.

Blattidae—Oriental, American, and other cockroaches
Polyphagidae (Cryptocercidae)*—sand cockroaches and others
Blattellidae—German, wood, and other cockroaches
Blaberidae—giant cockroaches and others

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[1] Blattodea: *blatta*, Latin for cockroach.

[2] Valuable contributions to this chapter made by Philippe Grandcolas.

Key to the Families of Blattodea

1.	Length 3 mm or less; found in ant nests	2*	
1′.	Length over 3 mm; almost never found in ant nests	3	
2(1).	Clypeus large and divided; found in association with carpenter ants (Formicinae: *Camponotus*) (*Myrmecoblatta*)	Polyphagidae*	p. 265
2′.	Clypeus small, undivided; found in association with leaf-cutter ants (Myrmicinae: Attini) (*Attaphila*)	Blattellidae*	p. 266
3(1′).	Middle and hind femora with numerous spines on ventroposterior margin	4	
3′.	Middle and hind femora without spines on ventroposterior margin, or with hairs and bristles only, or 1 or 2 apical spines	8	
4(3).	Pronotum and front wings densely covered with silky pubescence; length 27 mm or more (tropical species accidental in the United States: *Nyctibora*)	Blattellidae (in part)*	p. 266
4′.	Pronotum and front wings glabrous or only very sparsely pubescent	5	
5(4′).	Ventroposterior margin of front femora with row of spines that either decrease gradually in size and length distally or are nearly equal length throughout (Figure 21–1A)	6	
5′.	Ventroposterior margin of front femora with row of heavy spines proximally and more slender and shorter spines distally (Figure 21–1B)	7	
6(5).	Female subgenital plate divided longitudinally (Figure 21–2C); male styli similar, slender, elongate, and straight (Figure 21–2D); length 18 mm or more (*Blatta, Periplaneta, Eurycotis, Neostylopyga*)	Blattidae	p. 265
6′.	Female subgenital plate entire, not divided longitudinally (Figure 21–2B); male styli variable, often modified, asymmetrical, or unequal in size (Figure 21–2E); length variable, but usually less than 18 mm (*Supella, Cariblatta, Symploce, Pseudomops, Blattella*)	Blattellidae (in part)	p. 266
7(5′).	Front femora with only 1 apical spine; supra-anal plate weakly bilobed; glossy light brown, with sides and front of pronotum and basal costal part of front wings yellowish; 15–20 mm long; Florida Keys (*Phoetalia, Epilampra*)	Blaberidae (in part)*	p. 266
7′.	Front femora with 2 or 3 apical spines; supra-anal plate not bilobed; size and color variable; widely distributed (*Ectobius, Latiblattella, Ischnoptera, Parcoblatta, Euthlastoblatta, Aglaopteryx*)	Blattellidae (in part)	p. 266

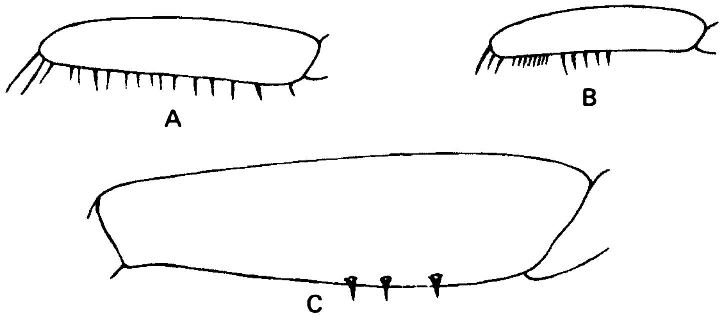


Figure 21–1 Front femora of Blattodea. A, *Periplaneta* (Blattidae); B, *Parcoblatta* (Blattellidae); C, *Blaberus* (Blaberidae).

8(3′).	Distal portion of abdomen (usually including cerci) covered by produced seventh dorsal and sixth ventral abdominal sclerites, subgenital plate absent; wingless, body almost parallel-sided, shining reddish brown, finely punctate, 23–29 mm in length; widely distributed, usually found in rotting logs (*Cryptocercus*)	Polyphagidae*	p. 265
8′.	Distal portion of abdomen not so covered, subgenital plate present; wings usually well developed (absent in some females); usually oval in shape; size and color variable; mostly southern United States	9*	
9(8′).	Hind wings with an apical portion (intercalated triangle or appendicular area) that folds over when wings are in resting position (Figure 21–2A, it); 8.5 mm in length or less, glossy yellowish, often beetlelike in appearance; southeastern United States (*Chorisoneura, Plectoptera*)	Blattellidae (in part)*	p. 266
9′.	Hind wings not as in preceding entry	10*	
10(9′).	Front femora with 1 to 3 spines on ventroposterior margin and 1 at tip (Figure 21–1C); length over 40 mm; arolia present; southern Florida (*Blaberus, Hemiblabera*)	Blaberidae (in part)*	p. 266
10′.	Front femora without spines on ventroposterior margin and with 1 or a few at tip; size variable; arolia present or absent; eastern and southern United States	11*	
11(10′).	Wings well developed, the anal area of hind wings folded fanwise at rest; frons flat, not bulging; length over 16 mm, pale green in color (*Panchlora, Pycnoscelus, Nauphoeta, Leucophaea*)	Blaberidae (in part)*	p. 266
11′.	Anal area of hind wings flat, not folded fanwise at rest (some females are wingless); frons thickened and somewhat bulging; usually (except some *Arenivaga*) less than 16 mm in length and never green (*Holocompsa, Eremoblatta, Compsodes, Arenivaga*)	Polyphagidae*	p. 265

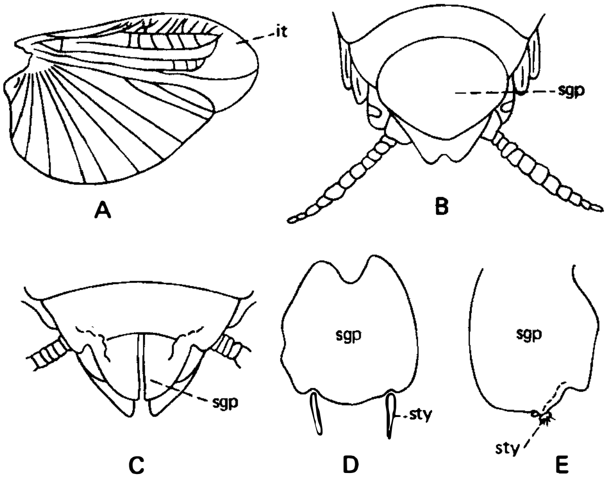


Figure 21–2 A, hind wing of *Chorisoneura* (Blattellidae); B, apex of abdomen of female cockroach (Blattellidae), ventral view; C, apex of abdomen of female cockroach (Blattidae), ventral view; D, subgenital plate of male cockroach (Blattidae), ventral view; E, same (Blattellidae). *it*, intercalated triangle; *sgp*, subgenital plate; *sty*, stylus.

Family **Blattidae:** The cockroaches in this group are relatively large insects (most are 25 mm or more in length). Several species are important household pests. One of the most common pest species in this group is the Oriental cockroach, *Blatta orientalis* L., which is about 25 mm long, dark brown, and broadly oval with short wings (Figure 21–3D,E). Several species of *Periplaneta* also invade houses, one of the most common being the American cockroach, *P. americana* (L.) (Figure 21–3B). This species is about 27–35 mm long and reddish brown, with well-developed wings. *Eurycotis floridana* (Walker) is found in Florida and southernmost Mississippi, Alabama, and Georgia. It lives under various sorts of cover outdoors, emits a very smelly liquid, and is sometimes called the "stinking cockroach." It is brown to black, with very short wings, and 30–39 mm in length.

Family **Polyphagidae:** These are mostly small cockroaches that have a rather hairy pronotum. In the winged forms, the anal area of the hind wings is flat at rest (not folded fanwise). They occur in the southern states, from Florida to California. Most species in the Southwest (*Arenivaga* and *Eremoblatta*) are in desert ar-

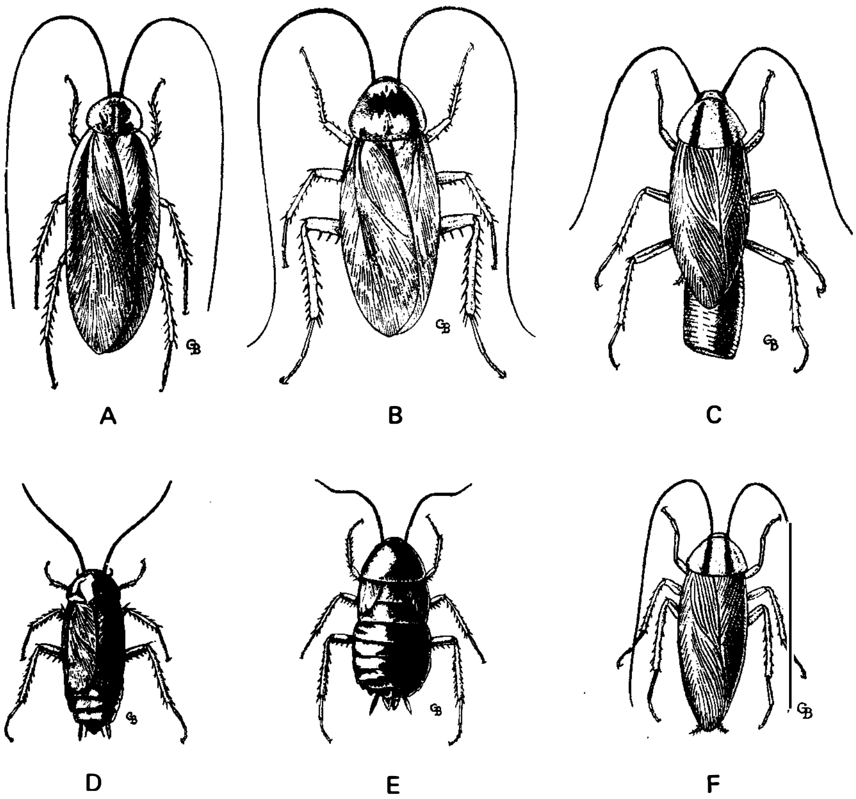


Figure 21–3 Some common cockroaches. A, a wood cockroach, *Parcoblatta pennsylvanica* (DeGeer) (Blattellidae); B, the American cockroach, *Periplaneta americana* (L.) (Blattidae); C, the German cockroach, *Blattella germanica* (L.), female (Blattellidae); D, the oriental cockroach, *Blatta orientalis* (L.), male (Blattidae); E, same, female; F, the German cockroach, male. A, slightly enlarged; B, D, and E, about natural size; C and F, 2×. (Courtesy of Institut de Biologie Générale, Université de Montréal.)

eas (some burrow in the sand like moles), and the females are wingless. Some *Arenivaga* are nearly 25 mm in length. Other species are 6.5 mm in length or less.

The brown-hooded cockroach, *Cryptocercus punctulatus* Scudder, is a subsocial species that occurs in hilly or mountainous areas from Pennsylvania to Georgia and Alabama in the East and from Washington to northern California in the West. This cockroach is wingless, 23–29 mm in length, and shining reddish brown with the dorsal surface finely punctured and is somewhat elongate and parallel-sided. It occurs in decaying logs, particularly oak logs. This cockroach has intestinal protists that break down the cellulose ingested (as in termites). *Cryptocercus* traditionally has been placed in its own family Cryptocercidae. We follow here the phylogenetic results of Grandcolas and D'Haese (2001) in grouping them in the Polyphagidae.

***Family* Blattellidae:** This is a large group of small cockroaches, most of them 12 mm in length or less. Several species invade houses. One of the most important of these is the German cockroach, *Blattella germanica* (L.) (Figure 21–3C,F), which is light brown with two longitudinal stripes on the pronotum. Another is the brown-banded cockroach, *Supella longipalpa* (Fabricius). A number of species in this group occur outdoors; the most common such species in the North are the wood cockroaches, *Parcoblatta* spp. (Figure 21–3A), which live in litter and debris in woods. Most species in this group occur in the South, where they may be found in litter and debris outdoors, under signs on trees, and in similar situations. The Asian cockroach, *Blattella asahinae* Mizukoba, morphologically very similar to *B. germanica*, is now established in Florida (first detected in 1986). *Attaphila fungicola* Wheeler is 3 mm long or less and lives in southern Texas and Louisiana in the nests of leaf-cutting ants. The proper classification of this small and behaviorally specialized genus is uncertain.

***Family* Blaberidae:** This group is principally tropical, and eleven North American species are nearly all restricted to the southern states. The group includes the largest U.S. cockroaches (*Blaberus* and *Rhyparobia*), which may reach a length of 50 mm. Most species are brownish, but one living in southern Texas east to Florida, *Panchlora nivea* (L.), is pale green. Most members of this group are found outside in litter or debris. A few occasionally get into houses, such as the Surinam cockroach, *Pycnoscelus surinamensis* (L.), and the Madeira cockroach, *Rhyparobia maderae* (Fabricius). The Madeira cockroach (38–51 mm in length) can stridulate, and it gives off an offensive odor.

Collecting and Preserving Blattodea

Cockroaches are mainly nocturnal creatures, and night is often the best time to collect them. They can be found by searching in leaf litter or under bark, or by overturning fallen logs. Many species, including the common household pests, can be caught by putting molasses or a similar bait in the bottom of a trap like that shown in Figure 35–6A. The insects so collected can simply be picked out of the trap.

Most nymphs and some soft-bodied adult specimens should be preserved in alcohol, but most adults can be pinned. Place the pin through the right tegmen, in about the middle (from front to rear) of the body. If the specimen is very soft-bodied, support the body by a piece of cardboard or by pins, or it will sag at either end.

References

Atkinson, T. H., P. G. Koehler, and R. S. Patterson. 1991. Catalogue and atlas of the cockroaches of North America north of Mexico. Misc. Publ. Entomol. Soc. Amer. 78:1–85.

Deyrup, M., and F. W. Fisk. 1984. A myrmecophilous cockroach new to the United States (Blattaria: Polyphagidae). Ent. News 95:183–185.

Fisk, F. W. 1987. Order Blattodea. In F. W. Stehr (Ed.), Immature Insects, vol. 1, pp. 120–131. Dubuque, IA: Kendall/Hunt, 754 pp.

Grandcolas, P. 1996. The phylogeny of cockroach families: A cladistic appraisal of morpho-anatomical data. Can. J. Zool. 74:508–527.

Grandcolas, P., and C. D'Haese. 2001. The phylogeny of cockroach families: is the current molecular hypothesis robust? Cladistics 12:93–98.

Hebard, M. 1917. The Blattidae of North America north of the Mexican boundary. Mem. Amer. Entomol. Soc. 2:1–284.

Helfer, J. R. 1987. How to Know the Grasshoppers, Cockroaches, and Their Allies, 2nd ed. New York: Dover Publications, 363 pp.

McKittrick, F. A. 1964. Evolutionary studies of cockroaches. Cornell Univ. Agr. Exp. Sta. Mem. No. 189, 197 pp.

McKittrick, F. A. 1965. A contribution to the understanding of the cockroach–termite affinities. Ann. Entomol. Soc. Amer. 58:18–22.

Princis, K. 1960. Zur Systematik der Blattarien. Eos, Revista Española Entomol. 36(4):427–449.

Princis, K. 1969. Fam. Blattellidae. Orthopterorum Catalogus 13:713–1038.

Rehn, J. W. H. 1950. A key to the genera of North American Blattaria, including established adventives. Entomol. News 61(3):64–67.

Rehn, J. W. H. 1951. Classification of the Blattaria as indicated by their wings (Orthoptera). Mem. Amer. Entomol. Soc. No. 14, 134 pp.

Roth, L. M. 1970. Evolution and taxonomic significance of reproduction in Blattaria. Annu. Rev. Entomol. 15:75–96.

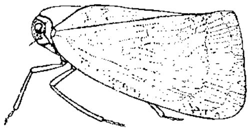
Roth, L. M., and E. R. Willis. 1957. The medical and veterinary importance of cockroaches. Smithson. Misc. Coll. 134(10), 147 pp.

Thorne, B. L., and J. M. Carpenter. 1992. Phylogeny of the Dictyoptera. Syst. Entomol. 17:253–268.

Vickery, V. R., and D. K. McKevan. 1985. The Grasshoppers, Crickets, and Related Insects of Canada and Adjacent Regions: Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera. The Insects and Arachnids of Canada, Part 14. Ottawa: Canadian Government Publishing Centre, 918 pp.

22

Order Hemiptera[1,2]
True Bugs, Cicadas, Hoppers, Psyllids, Whiteflies, Aphids, and Scale Insects



This is a large and diverse group of insects, varying considerably in body form, wings, antennae, life histories, and food habits. Many plant parasitic species are simplified in structure, lacking wings, eyes, and antennae. Given this diversity, it is not surprising that earlier authorities recognized two orders for these insects—the Hemiptera, or true bugs, and the Homoptera, including cicadas, hoppers, aphids, and their allies. Earlier classifications had the Homoptera divided into two suborders, the Auchenorrhyncha, containing the cicadas and hoppers, and the Sternorrhyncha, including the psyllids, whiteflies, aphids, and scale insects.

The most unifying character in this mélange of diversity is the mouthparts, which are of a unique piercing-sucking type (Figure 2–17). These consist of four piercing stylets (the mandibles and maxillae) enclosed in a slender, flexible sheath (the labium), which is usually segmented. The maxillae fit together in the beak to form two channels, a food channel and a salivary channel. There are no palps, although some authorities think that certain lobe-like structures on the beak of some aquatic bugs represent vestigial palps. The mouthparts of the Hemiptera are usually used for sucking plant sap, but in many of the true bugs they are used for sucking blood (for example, Reduviidae). The beak arises from the front of the head (Figure 22–1B) in the suborder Heteroptera, from the back of the head in the suborder Auchenorryhncha, and (when present) from between the procoxae in the Sternorrhyncha.

The front wings of the Heteroptera (if present) are usually very distinctive, consisting of a hardened or thickened basal portion and a membranous apical portion. This type of wing is called a *hemelytron* (plural, *hemelytra*). The hind wings are entirely membranous and slightly shorter than the front ones. The wings at rest are held flat over the abdomen with the membranous apical portions overlapping. Winged Auchenorrhyncha and Sternorrhyncha usually have four wings. The front wings have a uniform texture throughout, either membranous or slightly thickened, and the hind wings are membranous. The wings at rest are held roof-like over the body, with the inner margins slightly overlapping at the apex. In some groups one or both sexes may be wingless, or both winged and wingless individuals may occur in the same sex. Male scale insects have only one pair of wings, located on the mesothorax.

The Hemiptera usually undergo simple metamorphosis. The development in whiteflies and scale insects resembles complete metamorphosis in that the last nymphal instar is quiescent and pupa-like.

The life histories of some Sternorrhyncha are very complex, involving bisexual and parthenogenetic generations, winged and wingless individuals, and generations, and sometimes regular alternation of food plants. Some species transmit plant diseases and a few Heteroptera are vectors of diseases of warm-blooded vertebrates, including humans. Many species are serious pests of cultivated plants. A few provide useful products such as shellac, dyes, and other materials.

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[1] Hemiptera: *hemi*, half; *ptera*, wings, referring to the characteristic of the Heteroptera in which the front wings usually have the basal portion thickened and the distal portion membranous.

[2] The Heteroptera section of this chapter was edited by James A. Slater, the Coccoidea section by Michael Kosztarab, and the Cicadidae section by Thomas E. Moore.

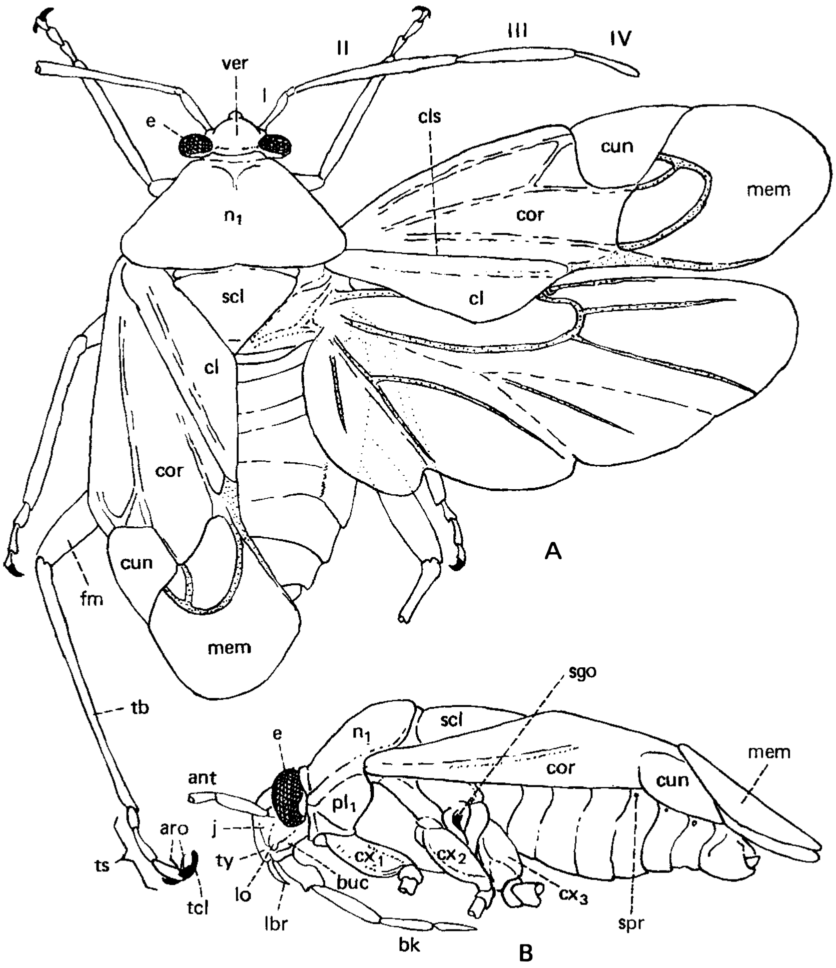


Figure 22–1 Structure of a plant bug, *Lygus oblineatus* (Say), family Miridae. A, dorsal view; B, lateral view. *ant*, antenna; *aro*, arolia; *bk*, beak; *buc*, buccula; *cl*, clavus; *cls*, claval suture; *cor*, corium; *cun*, cuneus; *cx*, coxa; *e*, compound eye; *fm*, femur; *j*, jugum; *lbr*, labrum; *lo*, lorum; *mem*, membrane; n_1, pronotum; pl_1, propleuron; *scl*, scutellum; *sgo*, scent gland opening; *spr*, spiracle; *tb*, tibia; *tcl*, tarsal claw; *ts*, tarsus; *ty*, tylus; *ver*, vertex; *I–IV*, antennal segments.

Classification of the Hemiptera

The classification of the true bugs, or Heteroptera, follows Schuh and Slater (1995) with the inclusion of superfamilies as listed in Henry and Froeschner (1988).

- Suborder Heteroptera
  - Infraorder Enicocephalomorpha
    - Superfamily Enicocephaloidea
      - Aenictopecheidae
      - Enicocephalidae—unique-headed bugs, gnat bugs
  - Infraorder Dipsocoromorpha
    - Superfamily Dipsocoroidea
      - Ceratocombidae
      - Dipsocoridae—jumping ground bugs
      - Schizopteridae—jumping ground bugs
  - Infraorder Gerromorpha
    - Superfamily Hebroidea
      - Hebridae—velvet water bugs
    - Superfamily Mesovelioidea
      - Mesoveliidae—water treaders
    - Superfamily Hydrometroidea
      - Macroveliidae
      - Hydrometridae—water measurers, marsh treaders
    - Superfamily Gerroidea
      - Veliidae—broad-shouldered water striders, riffle bugs
      - Gerridae—water striders
  - Infraorder Nepomorpha
    - Superfamily Nepoidea
      - Belastomatidae—giant water bugs
      - Nepidae—waterscorpions

- Superfamily Gelastocoroidea
  - Gelastocoridae—toad bugs
  - Ochteridae—velvety shore bugs
- Superfamily Corixoidea
  - Corixidae—water boatmen
- Superfamily Naucoroidea
  - Naucoridae—creeping water bugs
- Superfamily Notonectoidea
  - Notonectidae—backswimmers
  - Pleidae—pygmy backswimmers

Infraorder Leptopodomorpha
- Superfamily Leptopodoidea
  - Saldidae—shore bugs
  - Leptopodidae—spiny shore bugs

Infraorder Cimicomorpha
- Superfamily Reduvioidea
  - Reduviidae (including Phymatidae, Ploiariidae)—assassin bugs, ambush bugs, thread-legged bugs
- Superfamily Thaumastocoroidea
  - Thaumastocoridae—royal palm bugs
- Superfamily Miroidea
  - Microphysidae
  - Miridae—leaf bugs, plant bugs
- Superfamily Tingoidea
  - Tingidae—lace bugs
- Superfamily Cimicoidea
  - Nabidae—damsel bugs
  - Lasiochilidae
  - Lyctocoridae
  - Anthocoridae—minute pirate bugs
  - Cimicidae—bed bugs
  - Polyctenidae—bat bugs

Infraorder Pentatomomorpha
- Superfamily Aradoidea
  - Aradidae—flat bugs
- Superfamily Pentatomoidea
  - Acanthosomatidae
  - Cydnidae—burrower bugs
  - Pentatomidae—stink bugs
  - Scutelleridae—shield-backed bugs
- Superfamily Lygaeoidea
  - Berytidae—stilt bugs
  - Rhyparochromidae
  - Lygaeidae—seed bugs
  - Blissidae
  - Ninidae
  - Cymidae
  - Geocoridae—big-eyed bugs
  - Artheneidae
  - Oxycarenidae
  - Pachygronthidae
  - Heterogastridae
- Superfamily Piesmatoidea
  - Piesmatidae—ash-gray leaf bugs
- Superfamily Pyrrhocoroidea
  - Largidae
  - Pyrrhocoridae—red bugs, cotton stainers
- Superfamily Coreoidea
  - Alydidae—broad-headed bugs
  - Coreidae—squash bugs, leaf-footed bugs
  - Rhopalidae—scentless plant bugs

Suborder Auchenorrhyncha
- Superfamily Cicadoidea
  - Cicadidae—cicadas
  - Cercopidae—froghoppers, spittlebugs
  - Aetalionidae
  - Membracidae—treehoppers
  - Cicadellidae—leafhoppers
- Superfamily Fulgoroidea
  - Delphacidae
  - Cixiidae
  - Fulgoridae
  - Achilidae
  - Derbidae
  - Dictyopharidae
  - Tropiduchidae
  - Kinnaridae
  - Issidae (including Acanaloniidae)
  - Flatidae

Suborder Sternorrhyncha
- Superfamily Psylloidea
  - Psyllidae—psyllids, jumping plantlice
- Superfamily Aleyrodoidea
  - Aleyrodidae—whiteflies
- Superfamily Aphidoidea
  - Aphididae (including Eriosomatidae)—aphids, plantlice
  - Phylloxeridae
  - Adelgidae—pine and spruce aphids
- Superfamily Coccoidea
  - Margarodidae—giant coccids, ground pearls
  - Ortheziidae—ensign coccids
  - Pseudococcidae—mealybugs
  - Eriococcidae—felt scales
  - Cryptococcidae—bark-crevice scales
  - Kermesidae—gall-like coccids
  - Dactylopiidae—cochineal insects
  - Asterolecaniidae—pit scales
  - Cerococcidae—ornate pit scales
  - Lecanodiaspididae—false pit scales
  - Aclerdidae—grass scales
  - Coccidae—soft scales, wax scales, tortoise scales
  - Kerriidae (Tachardiidae)—lac scales
  - Phoenicococcidae—date scales
  - Conchaspididae—false armored scales
  - Diaspididae—armored scales

Characters Used in Identifying Hemiptera

The principal characters used in separating the families of the Heteroptera are those of the antennae, beak, legs, and wings. Features of the thorax and abdomen (particularly the symmetry or asymmetry of the genitalia, the nature of the phallus and spermatheca, and the position of the spiracles and trichobothria), and such general characters as size, shape, color, and habitat are sometimes used in separating families.

The antennae may be either four- or five-segmented. In a few Heteroptera, such as some of the Reduviidae, one of the antennal segments may be divided into several subsegments. In counting the antennal segments, the minute segments between the larger ones are not counted. In the Nepomorpha, the antennae are very short and concealed in grooves on the underside of the head; in the other infraorders, they are fairly long and conspicuous. The beak is usually three- or four-segmented and in some groups fits into a groove on the prosternum when not in use. In the Pentatomoidea, the five-segmented antennae are often hidden beneath a ridge on the side of the head.

The posterolateral angles of the pronotum are sometimes called the *humeral angles,* or the *humeri.* The disk is the central dorsal portion of the pronotum. It sometimes bears slightly raised areas (the calli) anteriorly. In some cases the anterior border of the pronotum is more or less separated from the rest of the pronotum by a groove or suture, thus forming a collar. A few Heteroptera have a more-or-less two-part pronotum, or divided into an anterior and a posterior lobe (for example, Figures 22–31C, 22–35B,F). Laterally the pronotum may have a sharp edge (in which case it is described as "margined") or it may be rounded.

The front legs in many predaceous Heteroptera are more or less modified into grasping structures and are spoken of as being *raptorial.* A raptorial leg (Figure 22–2) usually has the femur enlarged and armed with large spines on the ventroposterior margin. The tibia fits tightly against this armed surface, and often it, too, bears conspicuous spines.

The Heteroptera generally have two or three tarsal segments, the last of which bears a pair of claws. The claws are apical in most of the Heteroptera, but in the water striders (Gerridae and Veliidae) they are anteapical; that is, they arise slightly proximad of the tip of the last tarsal segment (Figure 22–3C,D). Many Heteroptera have arolia, or lobelike pads, one at the base of each tarsal claw (Figure 22–3A, aro).

The hemelytra differ considerably in different groups of bugs, and entomologists give special names to its different parts (Figure 22–4). The thickened basal part of the hemelytron consists of two sections, the corium (cor) and clavus (cl), which are separated by the claval suture (cls). The thin apical part of the hemelytron is the membrane (mem). In some Heteroptera, a narrow strip of the corium along the costal margin is set off from the remainder of the corium by a suture; this is the embolium (Figure 22–4C, emb). In a few Heteroptera, a cuneus (Figure 22–4A, cun) is set off by a suture in the apical part of the corium. The membrane usually contains veins, the number and arrangement of which often serve to separate different families.

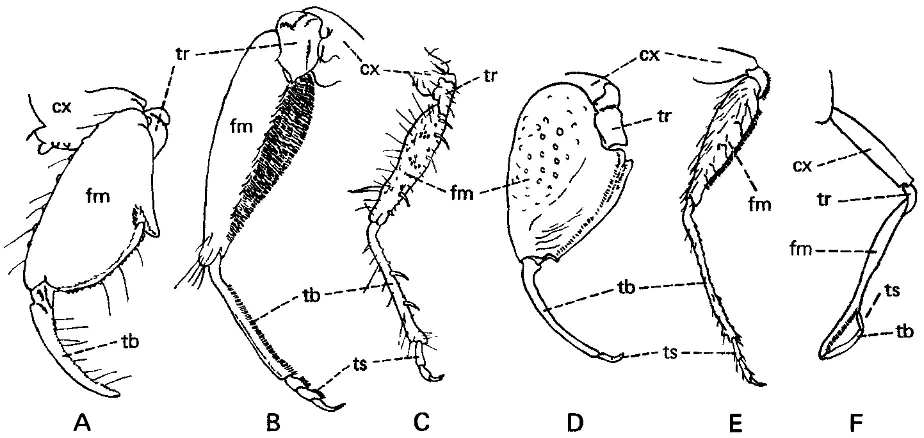


Figure 22–2 Raptorial front legs of Hemiptera. A, *Phymata* (Reduviidae); B, *Lethocerus* (Belostomatidae); C, *Sinea* (Reduviidae); D, *Pelocoris* (Naucoridae); E, *Nabis* (Nabidae); F, *Ranatra* (Nepidae). *cx*, coxa; *fm*, femur; *tb*, tibia; *tr*, trochanter; *ts*, tarsus.

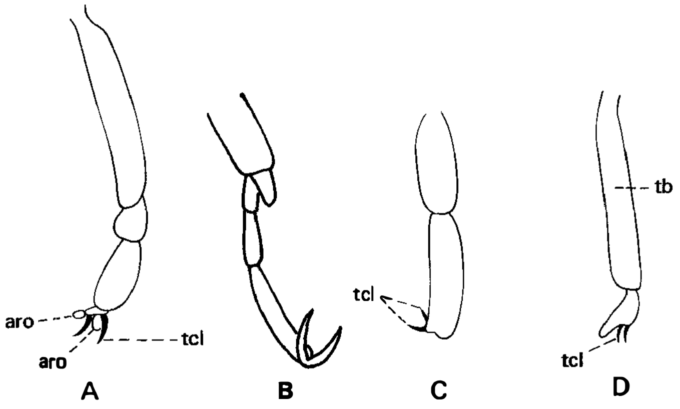


Figure 22–3 Tarsi of Hemiptera. A, hind tarsus of *Lygaeus* (Lygaeidae); B, middle tarsus of *Nabis* (Nabidae); C, front tarsus of *Gerris* (Gerridae); D, front tarsus and tibia of *Rhagovelia* (Veliidae). *aro*, arolia; *tb*, tibia; *tcl*, tarsal claw.

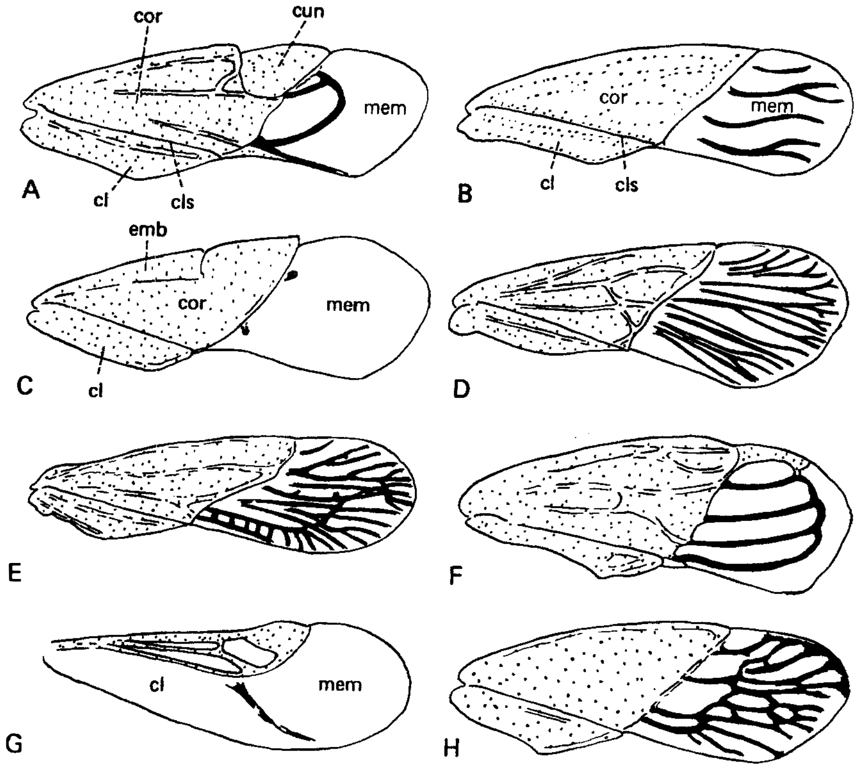


Figure 22–4 Hemelytra of Heteroptera. A, *Lygus* (Miridae); B, *Ligyrocoris* (Rhyparochromidae); C, *Orius* (Anthocoridae); D, *Boisea* (Rhopalidae); E, *Nabis* (Nabidae); F, *Saldula* (Saldidae); G, *Mesovelia* (Mesoveliidae); H, *Largus* (Largidae). *cl*, clavus; *cls*, claval suture; *cor*, corium; *cun*, cuneus; *emb*, embolium; *mem*, membrane.

In the Auchenorrhyncha, the main characters used in separating families involve the ocelli, the position of the antennae, the form of the pronotum, the spination of the legs, and the texture and venation of the wings.

The Sternorrhyncha are separated on the basis of the number of tarsal and antennal segments; the structure, texture, and venation of the wings; and other characters. Scale insects are separated on the characters of the adult female. They generally must be mounted on microscope slides to run them through the key (see procedures for collecting and preserving, at the end of the chapter).

Key to the Families of Hemiptera

This key is based on adults, but it will work for some nymphs. There should be no particular difficulty in identifying winged specimens, but the brachypterous and wingless forms may be troublesome. Some wingless Aphidoidea can be separated only if one is familiar with their life history. Families marked with an asterisk are relatively rare or are unlikely to be taken by a general collector.

1.	Beak arising from back of head or apparently from between front coxae; antennae variable (bristlelike or with more than 5 segments); front wings of uniform texture throughout, held roof-like over abdomen, tips not or but slightly overlapping	2	
1′.	Beak arising from front part of head; antennae 4- or 5-segmented, not bristlelike; front wings (if present) usually thickened at base, membranous apically, the membranous portions overlapping at rest; hind wings uniformly membranous (suborder Heteroptera)	3	
2(1).	Antennal flagellum short, bristlelike; beak arising from back of head; tarsi 3-segmented; active, free-living insects (suborder Auchenorrhyncha)	65	
2′.	Antennae usually long and filiform, with evident segmentation; beak, when present, arising between front coxae; tarsi (when legs are present), arising between front coxae; often not active insects (suborder Sternorrhyncha)	81	
3(1′).	Compound eyes absent	**Polyctenidae***	p. 296
3′.	Compound eyes present	4	
4(3′).	Head constricted transversely, divided into 2 distinct lobes; ocelli (when present) placed on posterior lobe; forewings of uniform texture throughout, not divided into corium and membrane (infraorder Enicocephalomorpha)	5	
4′.	Head usually not constricted and not divided into lobes; forewings usually divided into a distinct corium and membrane	6	
5(4).	Posterior pronotal lobe reduced, just distinguishable in lateral outline; macropters with a short costal fracture; ovipositor present; parameres distinct and movable	**Aenictopecheidae**	p. 288
5′.	Posterior pronotal lobe not reduced, well differentiated in lateral view; macropters lacking a costal fracture; ovipositor lacking or vestigial; parameres invisible	**Enicocephalidae**	p. 288
6(4′).	Antennae shorter than head, usually hidden in cavities beneath eyes (Figure 22–5A); no arolia; aquatic or semiaquatic (infraorder Nepomorpha)	7	
6′.	Antennae as long as or longer than head, usually free and visible from above; arolia present or absent; habits variable	14	
7(6).	Ocelli present (Figure 22–5B); length 10 mm or less	8	
7′.	Ocelli absent; size variable; aquatic species	9	

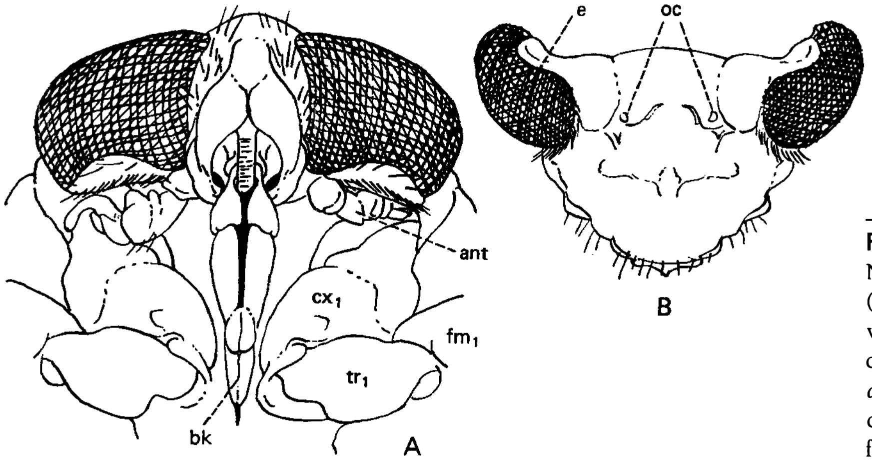


Figure 22–5 Head structure in Nepomorpha. A, *Lethocerus* (Belostomatidae), ventroanterior view; B, *Gelastocoris* (Gelastocoridae), dorsoanterior view. *ant*, antenna; *bk*, beak; *cx₁*, front coxa; *e*, compound eye; *fm*, femur; *oc*, ocelli; *tr*, trochanter.

8(7).	Antennae hidden; front legs shorter than middle legs; eyes strongly protuberant (Figure 22–21); beak short, concealed by front femora	Gelastocoridae	p. 290
8′.	Antennae exposed; front legs as long as middle legs; eyes not strongly protuberant; beak long, extending at least to hind coxae	Ochteridae*	p. 290
9(7′).	Front tarsi 1-segmented and modified into scoop-shaped structures (Figure 22–6); beak very short and hidden, appearing 1-segmented; dorsal surface of body usually with fine, transverse lines	Corixidae	p. 290
9′.	Front tarsi not as in preceding entry; beak segmentation clearly evident; dorsal surface of body not as in preceding entry	10	
10(9′).	Body with 2 long terminal filaments (Figure 22–18); tarsi 1-segmented	Nepidae	p. 289
10′.	Body without elongate terminal filaments or, at most, with short ones (Figure 22–19); tarsi variable	11	
11(10′).	Hind legs long and oarlike (Figure 22–23); hind tarsi without claws; length 5–16 mm	Notonectidae	p. 291
11′.	Hind legs not unusually lengthened; hind tarsi with claws; length variable	12	
12(11′).	Oval, beetlelike, convex, 3 mm long or less, front legs not raptorial	Pleidae*	p. 292
12′.	More than 3 mm long, often more than 20 mm; not strongly convex; front legs raptorial with femora thickened	13	

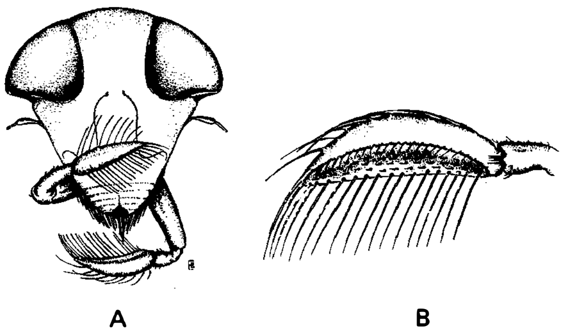


Figure 22–6 *Corixa* (Corixidae). A, head, anterior view; B, front leg. (Courtesy of Hungerford.)

13(12′).	Membrane of hemelytra with veins; abdomen with short terminal filaments (Figure 22–19); length over 20 mm	Belostomatidae	p. 289
13′.	Membrane of hemelytra without veins; abdomen without terminal filaments (Figure 22–22); length 5–16 mm	Naucoridae	p. 291
14(6′).	Body linear, head as long as entire thorax, and legs very slender (Figure 22–25); aquatic or semiaquatic	Hydrometridae	p. 292
14′.	Body of various forms, but if linear, then head shorter than thorax and the insect terrestrial	15	
15(14′).	Tarsal claws, especially on front legs, ante-apical (Figure 22–3C, D); apex of last tarsal segment more or less cleft; aquatic, surface inhabiting	16	
15′.	Tarsal claws apical; apex of last tarsal segment entire	17	
16(15).	Middle legs arising closer to hind legs than to front legs; hind femora extending well beyond apex of abdomen (Figure 22–26A); all tarsi 2-segmented; ocelli present but small;usually over 5 mm long	Gerridae	p. 293
16′.	Middle legs usually arising about midway between front and hind legs; if middle legs arise closer to hind legs than front legs (*Rhagovelia*), then front tarsi apparently 1-segmented (Figure 22–25B); hind femora extending little if any beyond apex of abdomen; tarsi 1-, 2-, or 3-segmented; ocelli absent, 1.6–5.5 mm long	Veliidae	p. 293
17(15′).	Antennae 4-segmented	18	
17′.	Antennae 5-segmented	58	
18(17).	Prosternum with a median, finely striated, longitudinal groove (Figure 22–7B, stg); beak short, 3-segmented, its tip fitting into prosternal groove; front legs usually raptorial	Reduviidae	p. 296
18′.	Prosternum without such a groove; beak longer, its tip not fitting into prosternal groove, 3- or 4-segmented; front legs variable	19	

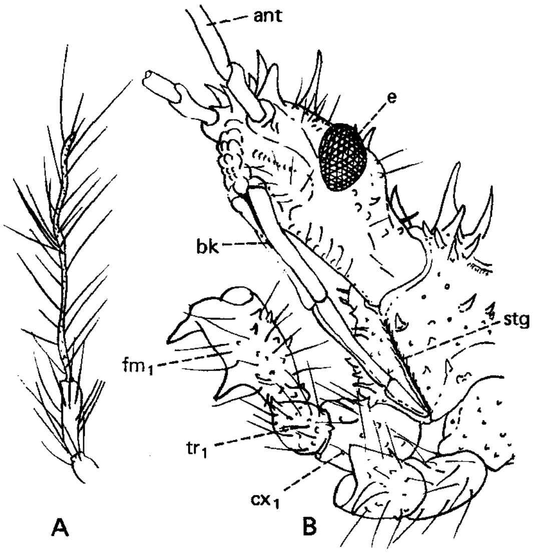


Figure 22–7 A, antenna of *Cryptostematida* (Dipsocoridae); B, head of *Sinea* (Reduviidae). *ant*, antenna; *bk*, beak; *cx*, coxa; *e*, compound eye; *fm*, femur; *stg*, prosternal groove; *tr*, trochanter.

19(18′).	Front wings with numerous closed cells (reticulately sculptured), without distinct division into corium, clavus, and membrane (Figure 22–27); pronotum with triangular process that extends back over scutellum; tarsi 1- or 2-segmented; ocelli absent; small somewhat flattened bugs, usually less than 5 mm long	Tingidae	p. 293
19′.	Front wings with variable arrangement of cells, but corium, membrane, and usually also clavus differentiated; pronotum usually without triangular process that extends back over scutellum; tarsi, ocelli, and size variable	20	
20(19′).	Ocelli present	21	
20′.	Ocelli absent	51	
21(20).	Tarsi, at least on hind legs, 2-segmented	22	
21′.	Tarsi, at least on hind legs, 3-segmented	26	
22(21).	Antennae with 2 basal segments short and thick, third and fourth segments very slender (Figure 22–7A); 2 mm long or less	26	
22′.	Not exactly fitting the description in preceding entry	23	
23(22′).	Clavus and membrane of hemelytra similar in texture (as in Figure 22–4G) (some are brachypterous); body densely clothed with short, velvety hairs; stout-bodied, semiaquatic bugs (*Merragata*)	Hebridae*	p. 292
23′.	Clavus and membrane of hemelytra different in texture; body not as in preceding entry	24	
24(23′).	Hemelytra with a cuneus; body shining black, 1.2 mm long; recorded from Maryland and the District of Columbia	Microphysidae*	p. 294
24′.	Hemelytra without a cuneus	25	
25(24′).	Corium and clavus reticulated, with an irregular network of small cells, juga extending considerably beyond tylus; pronotum with longitudinal ridges (Figure 22–33)	Piesmatidae	p. 298
25′.	Corium and clavus not as in preceding entry, juga not extending considerably beyond tylus; pronotum without longitudinal ridges	Thaumastocoridae*	p. 293
26(21′,22).	Antennae with 2 basal segments short and thick, third and fourth very slender (Figure 22–7A); tarsi and beak 3-segmented; length 3.5 mm or less	27	
26′.	Antennal segments similar, not as in preceding entry; tarsi and size variable	30	
27(26).	Head (including eyes), pronotum, front wings, front legs very spiny; third and fourth antennal segments not hairy; front femora thickened; 3–5 mm long; California	Leptopodidae*	p. 293
27′.	Body not spiny; third and fourth antennal segments hairy (Figure 22–7A); 1–2 mm long; widely distributed	28	
28(27′).	Proespisternal lobe broad in lateral view; mostly inflated and extending below eye articulation of forecoxa and basal part of latter covered; supracoxal cleft long	Schizopteridae*	p. 289
28′.	Proepisternal lobe narrow in lateral view, not inflated and not extending cephalad; articulation of forcoxae laterally exposed, supracoxal cleft extremely short to essentially absent	29	
29(28′).	Costal fracture short, just interrupting forewing margin, metapleuron without evaporatorium; male genitalia and abdomen symmetrical or asymmetrical, forewing terminal to brachypterous, or, rarely, coleopteroid	Ceratocombidae*	p. 289

29′.	Costal fracture reaching to about middle of width of forewing, metapleuron with evaporatorium; male genitalia and abdomen asymmetrical; forewing tegminal, macropterous to brachypterus	Dipsocoridae*	p. 289
30(26′).	Hemelytra with a cuneus; small to minute bugs, 1.2–5.0 mm long, usually 2–3 mm	31	
30′.	Hemelytra without a cuneus; size variable	34	
31(30).	Beak 4-segmented (Isometopinae)	Miridae	p. 294
31′.	Beak 3-segmented	32	
32(31′).	Abdominal terga 1 and 2 with laterotergites; terga 3 to 8 forming single plates; no traumatic insemination	Lasiochilidae*	p. 295
32′.	All abdominal terga with laterotergites; insemination traumatic	33	
33(32′).	Females with internal apophyses on anterior margin of abdominal sternum 7	Lyctocoridae*	p. 296
33′.	Females lacking apophyses on abdominal sternum 7	Anthocoridae	p. 296
34(30′).	Beak 3-segmented	35	
34′.	Beak 4-segmented	36	
35(34).	Membrane of hemelytra with 4 or 5 long, closed cells (Figure 22–4F)	Saldidae	p. 293
35′.	Membrane of hemelytra without veins, more or less confluent with the membranous clavus (Figures 22–4G, 22–24A)	Mesoveliidae*	p. 292
36(34′).	Bugs resembling mesoveliids in general appearance (Figure 22–24A), but with closed cells in the front wings, pronotum with a median backward projecting lobe that covers scutellum; western United States	Macroveliidae*	p. 292
36′.	Without the combination of characters in preceding entry	37	
37(36′).	Distal ends of front and middle tibiae with broad, flat apical process (Figure 22–3B); arolia absent; membrane of hemelytra (when developed) with numerous marginal cells (Figures 22–4E, 22–29A) (Nabinae)	Nabidae	p. 294
37′.	Distal ends of front and middle tibiae without such a process; arolia present (Figure 22–3A); membrane of hemelytra variable	38	
38(37′).	Body and appendages long and slender; first segment of antennae long and enlarged apically, last segment spindle-shaped; femora clavate (Figure 22–34)	Berytidae	p. 298
38′.	Body shape variable; antennae and femora not as in preceding entry	39	
39(38′).	Membrane of hemelytra with only 4 or 5 veins (Figure 22–4B)	40	
39′.	Membrane of hemelytra with many veins (Figure 22–4D)	49	
40(39).	Suture between abdominal sterna 4 and 5 usually curving forward laterally and rarely attaining lateral margin of abdomen; trichobothria usually present on head	Rhyparochromidae*	p. 298
40′.	Suture between abdominal sterna 4 and 5 not curving forward, attaining lateral margin of abdomen; no trichobothria present on head	41	
41(40′).	Spiracles on abdominal segments 2–7 all located dorsally	Lygaeidae	p. 299
41′.	At least one pair (and often more) of spiracles on abdominal segments 2–7 located ventrally	42	
42(41′).	Spiracles of abdominal segment 7 ventral, all others dorsal	43	
42′.	At least spiracles of abdominal segments 6 and 7 ventral	45	
43(42).	Hemelytra impunctate or at most with very faint, scattered punctures	Blissidae	p. 299
43′.	Hemelytra in large part coarsely punctate	44	
44(43′).	Apex of scutellum bifid; clavus in part hyaline; eyes somewhat stalked	Ninidae*	p. 300

44'.	Apex of scutellum pointed never bifid; clavus entirely coriaceous; eyes not on stalks	Cymidae	p. 300
45(42').	Spiracles of abdominal segments 3 and 4 dorsal	Geocoridae	p. 300
45'.	Spiracles of abdominal segments 3 to 7 ventral	46	
46(45').	Spiracles of abdominal segment 2 dorsal	47	
46'.	Spiracles of abdominal segment 2 ventral	48	
47(46).	Lateral pronotal margins explanate or laminate	Artheneidae*	p. 300
47'.	Lateral pronotal margins rounded or slightly carinate, never strongly explanate	Oxycarenidae	p. 300
48(46').	Fore femur strongly incrassate and heavily spined; no crossvein or closed cell basally in forewing membrane	Pachygronthidae*	p. 300
48'.	Fore femur at most weakly incrassate with a few small spines present; a closed cell present basally in base of forewing membrane	Heterogastridae*	p. 300
49(39').	Usually dark-colored, over 10 mm long; scent glands present, in opening between middle and hind coxae (Figure 22–1B, sgo)	50	
49'.	Usually pale-colored, less than 10 mm long; scent glands absent	Rhopalidae	p. 301
50(49).	Head narrower and shorter than pronotum (Figure 22–38A–C); bucculae (lateral view) extending backward beyond base of antennae; hind coxae more or less rounded or quadrate	Coreidae	p. 301
50'.	Head nearly as wide and as long as pronotum (Figure 22–38D); bucculae (lateral view) shorter, not extending backward beyond base of antennae; hind coxae more or less transverse	Alydidae	p. 301
51(20').	Tarsi 1-segmented; beak 3-segmented; front legs raptorial, the front femora slightly swollen; elongate, slender, 3.5–5.0 mm long, with constriction near middle of body; yellowish or greenish yellow with reddish brown markings; eastern United States (Carthasinae)	Nabidae*	p. 294
51'.	Tarsi 2- or 3-segmented; beak 3- or 4-segmented; front legs usually not raptorial; size, shape, color variable	52	
52(51').	Beak short, 3-segmented, fitting into groove in prosternum (Figure 22–7B); front femora more or less enlarged, raptorial; head more or less cylindrical, usually with transverse suture near eyes (Emesinae and Saicinae)	Reduviidae	p. 296
52'.	Beak longer, 3- or 4-segmented, not fitting into groove in prosternum; front femora and head variable	53	
53(52').	Beak 3-segmented; wings vestigial (Figure 22–30A); ectoparasites of birds and mammals	Cimicidae	p. 296
53'.	Beak 4-segmented (only 2–3 segments can be seen in some Aradidae); wings usually well developed	54	
54(53').	Hemelytra with cuneus, the membrane with 1 or 2 closed cells, rarely with other veins (Figure 22–4A); rarely (for example, *Halticus*; Figure 22–28A) membrane absent, in which case cuneus lacking; hind femora enlarged; mesosternum and metasternum formed of more than 1 sclerite	Miridae	p. 294
54'.	Hemelytra without cuneus, membrane not as in preceding entry; mesosternum and metasternum formed of a single sclerite	55	
55(54').	Tarsi without arolia; body very flat; usually dull-colored, gray, brown, or black (Figure 22–32)	Aradidae	p. 298
55'.	Tarsi with arolia; body not particularly flattened; often brightly colored	56	

56(55′).	Elongate, shining black bugs, 7–9 mm long; front femora moderately swollen and armed beneath with 2 rows of teeth (*Cnemodus*)	Lygaeidae	p. 299
56′.	Color variable, but usually not shining black; 8–18 mm long; front femora not swollen and usually not armed with teeth	57	
57(56′).	Pronotum margined laterally; sixth visible abdominal sternum entire in both sexes	Pyrrhocoridae	p. 300
57′.	Pronotum rounded laterally; sixth visible abdominal sternum of female cleft to base	Largidae	p. 300
58(17′).	Tarsi 2-segmented; body densely clothed with velvety pubescence; hemelytra with clavus and membrane similar in texture and without veins; the two basal antennal segments thicker than others; semiaquatic bugs, 3 mm long or less (*Hebrus*; Figure 22–24B)	Hebridae*	p. 292
58′.	Tarsi usually 3-segmented (2-segmented in Acanthosomatidae); body not covered with velvety pubescence; hemelytra with clavus and membrane differentiated, membrane usually with veins; the 2 basal antennal segments similar to others; terrestrial; usually over 3 mm long	59	
59(58′).	Apex of front and middle tibiae with broad, flat apical process (Figure 22–3B); scutellum only about one -fifth as long as abdomen; shining black bugs 5–7 mm long; body elongate and narrowed anteriorly, the pronotum distinctly narrower than the widest part of the abdomen (Prostemminae: *Pagasa*)	Nabidae*	p. 294
59′.	Apex of front and middle tibiae without such a process; size variable; color variable, but if shining black then body is oval or shield-shaped	60	
60(59′).	Tibiae armed with strong spines (Figure 22–8A); color usually shining black; length 8 mm or less	61	
60′.	Tibiae not armed with strong spines (Figure 22–8B); color rarely shining black; usually over 8 mm long	62	
61(60).	Scutellum very large, broadly rounded posteriorly, covering most of abdomen (Figure 22–39A); length usually 3–4 mm	Thyreocoridae	p. 302
61′.	Scutellum more or less triangular, not extending to apex of abdomen (Figure 22–39B); length up to about 8 mm	Cydnidae	p. 302
62(60′).	Scutellum very large, broadly rounded posteriorly, covering most of the abdomen (Figure 22–40); corium of hemelytra narrow, not extending to anal margin of wing	63	

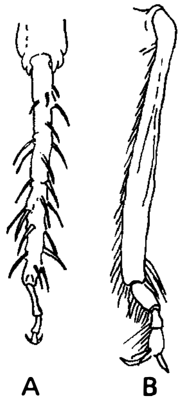


Figure 22–8 A, tibia of *Pangaeus* (Cydnidae); B, tibia of *Murgantia* (Pentatomidae).

62′.	Scutellum shorter, usually narrower posteriorly and more or less triangular (Figures 22–41, 22–42), if large and broadly rounded posteriorly (*Stiretrus*, family Pentatomidae, subfamily Asopinae), colors are bright and contrasting; corium of hemelytra broad, extending to anal margin of wing	64	
63(62).	Sides of pronotum with a prominent tooth or lobe in front of humeral angle (Figure 22–40B); length 3.5–6.5 mm (*Amaurochrous*)	Pentatomidae*	p. 302
63′.	Sides of pronotum without such a tooth or lobe (Figure 22–40A); length 8–10 mm	Scutelleridae	p. 302
64(62′).	Tarsi 2-segmented; sternum of thorax with median longitudinal ridge or keel	Acanthosomatidae	p. 303
64′.	Tarsi 3-segmented; sternum of thorax usually without median longitudinal keel	Pentatomidae	p. 302
65(2).	Antennae separated from front of head by a vertical carina, thus arising on sides of head beneath eyes (Figure 22–9C); tegulae usually present; 2 anal veins in front wing usually meeting apically to form a Y-vein (Figure 22–10A, B, clv) (Superfamily Fulgoroidea)	66	
65′.	Antennae not separated from front of head by a vertical carina, thus arising on front of head between eyes (Figures 22–9A, 22–49); tegulae usually absent, no Y-vein in anal area of front wing (Figures 22–11A, 22–12A) (superfamily Cicadoidea)	76	
66(65).	Hind tibiae with broad, movable apical spur (Figure 22–10C, sp); a large group of small to minute forms, many dimorphic (with wings well developed or short), the sexes often very different	Delphacidae	p. 315

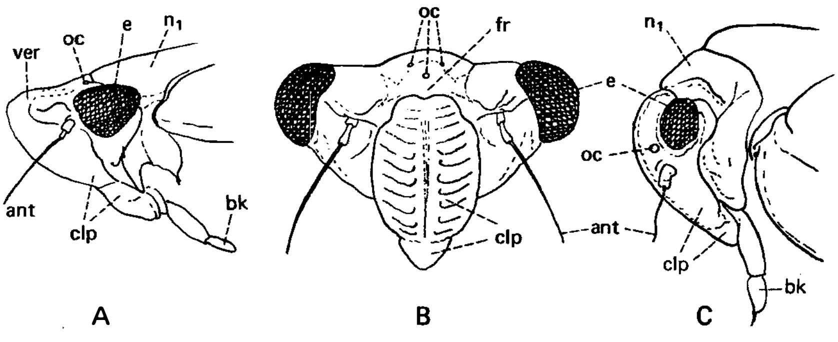


Figure 22–9 Head structure in Auchenorrhyncha. A, froghopper (Cercopidae: *Philaenus*), lateral view; B, cicada (Cicadidae: *Magicicada*), anterior view; C, planthopper (Flatidae: *Anormenis*), lateral view. *ant*, antenna; *bk*, beak; *clp*, clypeus; *e*, compound eye; *fr*, frons; n_1, pronotum; *oc*, ocelli; *ver*, vertex.

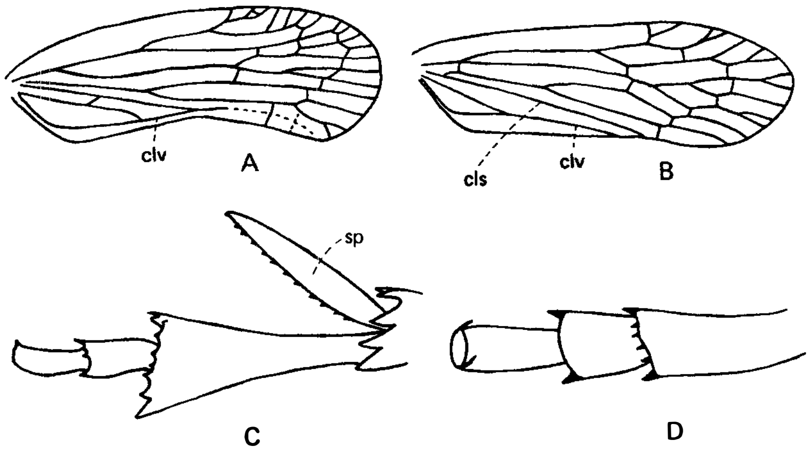


Figure 22–10 Characters of Fulgoroidea. A, front wing of *Epiptera* (Achilidae); B, front wing of *Cixius* (Cixiidae); C, hind tarsus of a delphacid; D, hind tarsus of *Anormenis* (Flatidae). *cls*, claval suture; *clv*, claval vein; *sp*, apical spur of tibia.

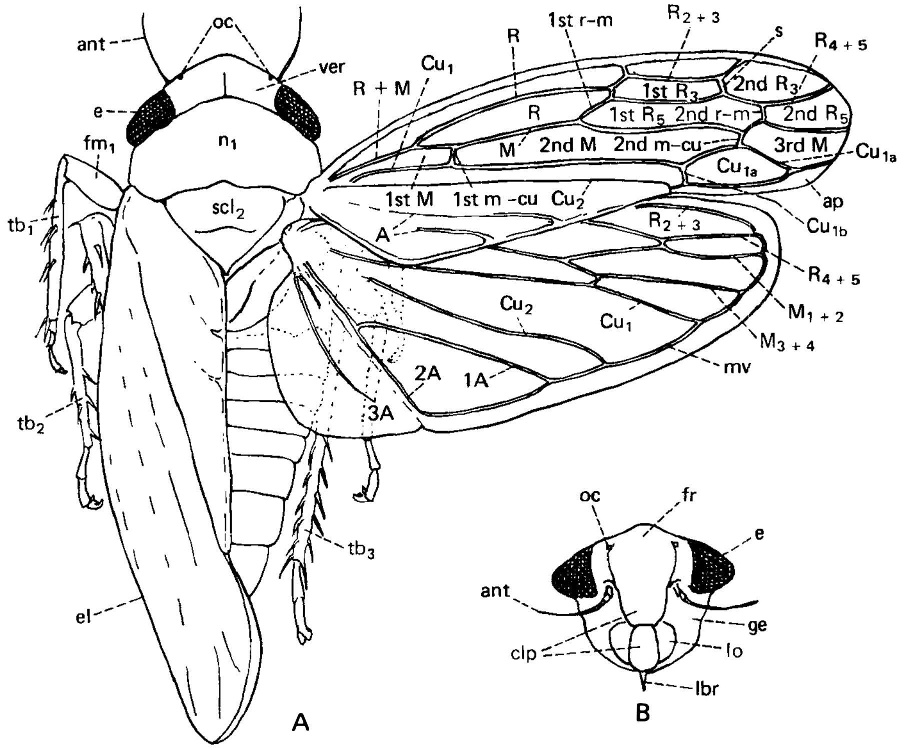


Figure 22–11 Structure of a leafhopper, *Paraphlepsius irroratus* (Say) (Cicadellidae). A, dorsal view; B, anterior view of head. *ant*, antennae; *ap*, appendix; *clp*, clypeus; *e*, compound eye; *el*, elytron or front wing; *fm*, femur; *fr*, frons; *ge*, gena; *lbr*, labrum; *lo*, lorum; *mv*, marginal vein; n_1, pronotum; *oc*, ocelli; scl_2, mesocutellum; *tb*, tibia; *ver*, vertex. The venational terminology follows the Comstock-Needham system, except for the veins posterior to the media. Students of the leafhoppers usually use a different terminology for the venational characters of the front wing; a comparison of their terminology with that used here is given in the following table.

Veins		Cells	
Terms in This Figure	Other Terms	Terms in This Figure	Other Terms
R + M	first sector	R	discal cell
R	outer branch of first sector	1st R_3	outer anteapical cell
M	inner branch of first sector	2nd R_3	first apical cell
Cu_1	second sector	1st R_5	anteapical cell
Cu_2	claval suture	2nd R_5	second apical cell
A	claval veins	2nd M	inner anteapical cell
1st m-cu	first crossvein	3rd M	third apical cell
2nd m-cu	apical crossvein	Cu_{1a}	fourth apical cell
s	apical crossvein		
1st r-m	crossvein between sectors		
2nd r-m	apical crossvein		

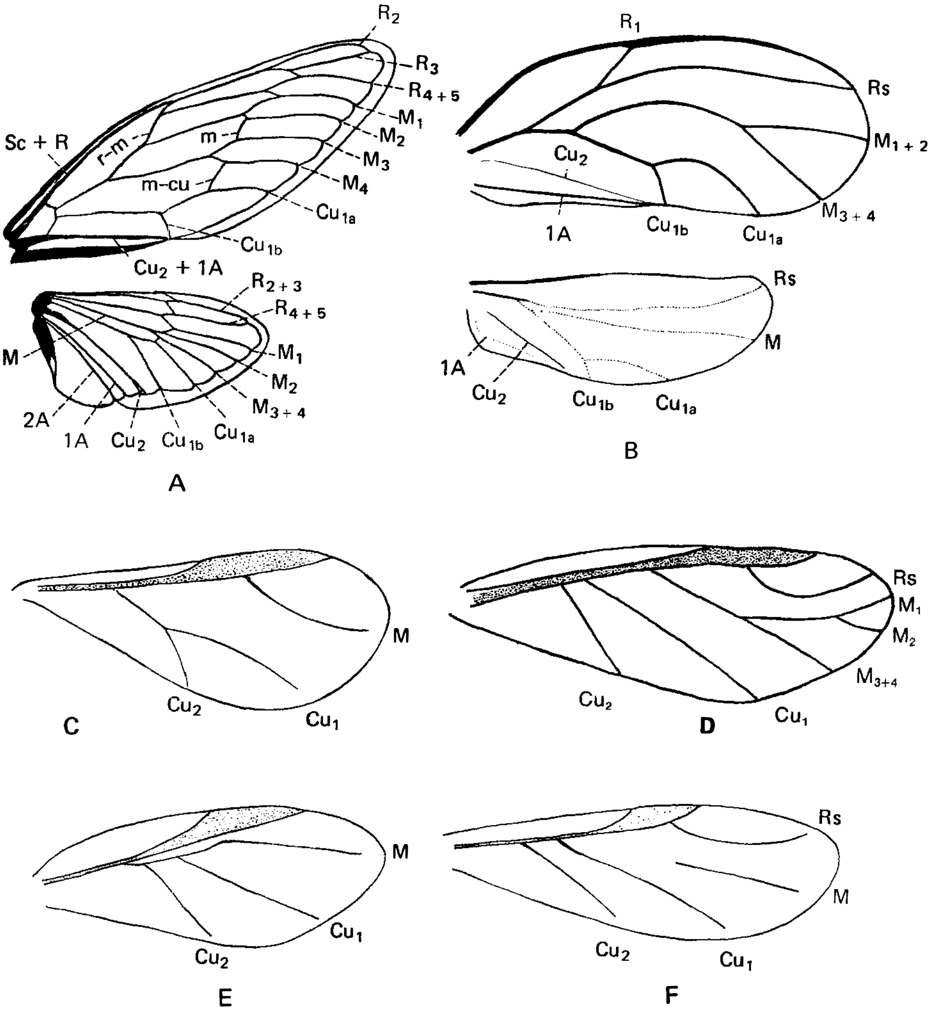


Figure 22–12 Wings of Auchenorrhyncha and Sternorrhyncha. A, Cicadidae (*Magicicada*); B, Psyllidae (*Psylla*); C, Phylloxeridae (*Phylloxera*); D, Aphididae (*Longistigma*); E, Adelgidae (*Adelges*); F, Aphididae (*Colopha*). C–F, front wings only.

66′.	Hind tibiae without broad, movable apical spur	67	
67(66′).	Anal area of hind wings reticulate, with many crossveins	Fulgoridae	p. 315
67′.	Anal area of hind wings not reticulate, without crossveins	68	
68(67′).	Second segment of hind tarsi with 2 apical spines (1 on each side) and with apex usually rounded or conical (Figure 22–10D)	69	
68′.	Second segment of hind tarsi with a row of apical spines and with apex truncate or emarginated	72	
69(68).	Front wings with numerous costal crossveins, longer than body, at rest held almost vertically at sides of body (Figure 22–51F); clavus with numerous small, pustulelike tubercles	Flatidae	p. 317

69′.	Front wings without numerous costal crossveins (except sometimes apically), variable in size and position at rest; clavus without numerous small, pustulelike tubercles	70	
70(69′).	Front wings longer than abdomen, with a series of crossveins between costal margin and apex of clavus separating off the apical, more densely veined portion of the wing; slender, greenish or yellowish to brownish, 7–9 mm long; southeastern United States, Florida to Louisiana	**Tropiduchidae**	p. 317
70′.	Front wings without differentiated apical portion as described in preceding entry; variable long	71	
71(70′).	Front wings very broad, venation reticulate, longer than body, at rest held almost vertically at sides of body (Figure 22–51E); hind tibiae without spines except at apex	**Acanaloniidae**	p. 317
71′.	Front wings variable in size and shape, often shorter than abdomen, but if longer than abdomen, then usually oval; hind tibiae usually with spines on sides, in addition to apical ones	**Issidae**	p. 317
72(68′).	Terminal segment of beak short, not more than 1.5 times as long as wide	**Derbidae**	p. 316
72′.	Terminal segment of beak longer, at least twice as long as wide	73	
73(72′).	Front wings overlapping at apex (Figure 22–51C); claval vein (a Y-vein) extending to apex of clavus (Figure 22–10A, clv); body somewhat flattened	**Achilidae**	p. 317
73′.	Front wings usually not overlapping at apex; claval vein not reaching apex of clavus (Figure 22–10B, clv); body not particularly flattened	74	
74(73′).	Head prolonged in front (Figure 22–51G–I), or if not, then frons bears 2 or 3 carinae, or the tegulae are absent and the claval suture is obscure; no median ocellus	**Dictyopharidae**	p. 317
74′.	Head not prolonged in front (Figure 22–51A,D) or only moderately so; frons either without carinae or with median carina only; tegulae present; claval suture distinct; median ocellus usually present	75	
75(74′).	Abdominal terga 6–8 chevron-shaped, sometimes sunk below rest of terga; 3-4 mm long; western United States	**Kinnaridae**	p. 317
75′.	Abdominal terga 6–8 rectangular; size variable; widely distributed	**Cixiidae**	p. 316
76(65′).	Three ocelli (Figure 22–9B); large insects with membranous front wings (Figure 22–43); males usually have sound-producing organs ventrally at base of abdomen (Figure 22–45); not jumping insects	Cicadidae	p. 305
76′.	Two (rarely 3) ocelli (Figure 22–11B) or none; smaller insects, sometimes with front wings thickened; sound-producing organs generally absent; usually jumping insects	77	
77(76′).	Pronotum extending back over abdomen and concealing the scutellum (Figure 22–46) or at least with a median backward-projecting process that partly conceals the scutellum (Figure 22–13A); hind tibiae usually without distinct spurs or long spines	78	
77′.	Pronotum not extending back over abdomen, the scutellum nearly always well exposed (Figures 22–13B, 22–47, 22–49); hind tibiae with or without distinct spurs or spines	79	
78(77).	Pronotum with a narrow, median, backward-projecting process that only partly conceals scutellum and extends between wings for one-fourth their length or less (Figure 22–13A), often with a pair of ridges or leaflike processes dorsally; beak extending to hind coxae (*Microcentrus*)	**Aetalionidae**	p. 307

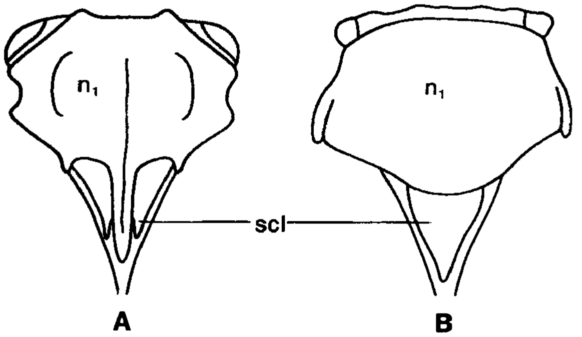


Figure 22–13 Pronotum and associated structures in Aetalionidae, dorsal view. A, *Microcentrus*; B, *Aetalion*. n_1, pronotum; *scl*, scutellum.

78′.	Pronotum broadly extended backward over wings and abdomen, completely covering scutellum and extending to middle wings or rather, often with spines or other processes or appearing arched (Figure 22–46); beak not extending to hind coxae	Membracidae	p. 306
79(77′).	Hind tibiae with 1 or more rows of small spines (Figure 22–14A); hind coxae transverse	Cicadellidae	p. 310
79′.	Hind tibiae without spines or with 1 or 2 stout ones laterally and a crown of short spines at tip (Figure 22–14B); hind coxae short and conical	80	
80(79′).	Hind tibiae without spines, but hairy; beak extending to hind coxae; head largely covered dorsally by pronotum (Figure 2–13B), the face vertical or nearly so; Florida, southern Arizona, and California (*Aetalion*)	Aetalionidae	p. 307
80′.	Hind tibiae with 1 or 2 stout spines laterally and a crown of short spines at tip (Figure 22–14B); head usually not largely covered by pronotum (Figure 22–47), the face slanting backward; beak length variable; widely distributed	Cercopidae	p. 309
81(2′).	Tarsi 2-segmented, with 2 claws; winged forms with 4 wings; mouthparts usually well developed in both sexes, with beak long	82	

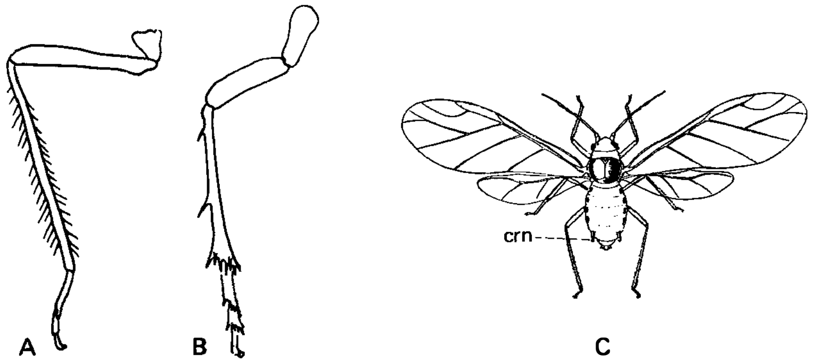


Figure 22–14 A, Hind leg of a leafhopper (Cicadellidae); B, hind leg of a froghopper (Cercopidae); C, a winged aphid (Aphididae). *crn*, cornicle. (C, Courtesy of USDA.)

81′.	Tarsi 1-segmented (rarely 2-segmented in males and some females of Margarodidae), with a single claw (when legs are present); female always wingless and often legless, scalelike, or grublike and wax-covered; male with only 1 pair of wings and without beak (superfamily Coccoidea)	86	
82(81).	Antennae with 5–10 (usually 10) segments; front wings often thicker than hind wings; jumping insects	Psyllidae	p. 317
82′.	Antennae with 3–7 segments; wings membranous or opaque whitish; not jumping insects	83	
83(82′).	Wings usually opaque, whitish, and covered with whitish powder; hind wings nearly as large as front wings; no cornicles	Aleyrodidae	p. 318
83′.	Wings membranous and not covered with whitish powder; hind wings much smaller than front wings (Figure 22–14C); cornicles often present (superfamily Aphidoidea)	84	
84(83′).	Front wings with 4 or 5 (rarely 6) veins behind stigma extending to wing margin (Rs present) (Figure 22–12D, F); cornicles usually present (Figure 22–14C); antennae generally 6-segmented; sexual females oviparous, parthenogenetic females viviparous	Aphididae	p. 319
84′.	Front wings with only 3 veins behind stigma extending to wing margins (Rs absent) (Figure 22–12C, E); cornicles absent; antennae 3- to 5-segmented; all females oviparous	85	
85(84′).	Wings at rest held rooflike over body; Cu_1 and Cu_2 in front wing separated at base (Figure 22–12E); apterous parthenogenetic females covered with waxy flocculence; on conifers	Adelgidae	p. 321
85′.	Wings at rest held horizontal; Cu_1 and Cu_2 in front wing stalked at base (Figure 22–12C); apterous parthenogenetic females not covered with waxy flocculence (at most, covered with a powdery material)	Phylloxeridae	p. 322
86(81′).	Abdominal spiracles present (Figure 22–15A, spr); male usually with compound eyes and ocelli	87	
86′.	Abdominal spiracles absent (Figure 22–16B); male with ocelli only	88	
87(86).	Anal ring distinct, with numerous pores and 6 long setae; antennae 3- to 8-segmented (Figure 22–15A)	Ortheziidae	p. 325
87′.	Anal ring reduced, without pores or setae;antennae 1- to 13-segmented	Margarodidae	p. 324
88(86′).	A large dorsal spine present near center of abdomen, anterior spiracles much larger than posterior ones; southwestern United States	Kerriidae	p. 327
88′.	No large dorsal spine in center of abdomen; all spiracles about equal in size; widely distributed	89	
89(88′).	Anal opening covered by 2 triangular plates (Figure 22–15D, anp) (except *Physokermes*); abdomen with well-developed anal cleft (Figure 22–15D, anc)	Coccidae	p. 324
89′.	Anal opening covered by single plate or none; anal cleft, if present, not well developed	90	
90(89′).	Anus covered by single oval or triangular plate; caudal margin of body with furrows or ridges; usually found under leaf sheaths of grasses and reeds	Aclerdidae	p. 326
90′.	No plate covering anal opening; caudal margin of body without furrows or ridges	91	
91(90′).	Anal ring surrounded by short, stout setae; cluster pore plate present, just below each posterior thoracic spiracle; northeastern United States, on sugar maple and beech trees	Cryptococcidae	p. 326

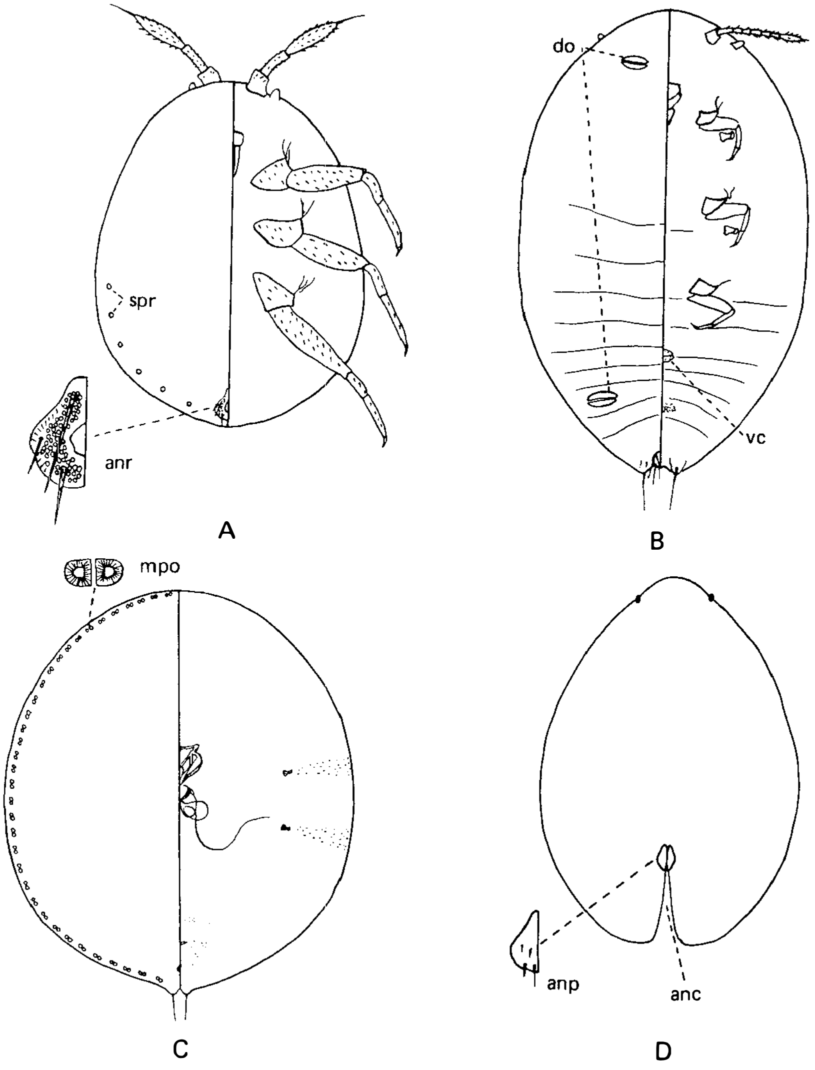


Figure 22–15 Characters of female scale insects (diagrammatic). A, Ortheziidae; B, Pseudococcidae; C, Asterolecaniidae; D, Coccidae. In A–C, the left side represents a dorsal view, and the right side a ventral view. *anc*, anal cleft; *anp*, anal plate; *anr*, anal ring; *do*, dorsal ostioles; *mpo*, marginal figure 8–shaped pores; *spr*, abdominal spiracles; *vc*, ventral circulus. (Figure prepared by Dr. Michael Kosztarab.)

91′.	Anal ring not surrounded by short, stout setae; no cluster pore plates; widely distributed, on various host plants	92	
92(91′).	Dorsum with figure 8–shaped pores (Figure 22–15C, mpo)	93	
92′.	Dorsum without figure 8–shaped pores	96	
93(92).	Figure 8–shaped pores on dorsum and in submarginal band on venter; antennae 1- to 9-segmented; on various host plants	94	
93′.	Figure 8–shaped pores restricted to dorsum; antennae 5-segmented; on oaks	Kermesidae	p. 326
94(93).	A sclerotized anal plate present; antennae 1- to 9-segmented	95	
94′.	No sclerotized anal plate present; antennae 1-segmented	Asterolecaniidae	p. 326
95(94).	Antennae 1-segmented, with associated cluster of 5–7 locular pores; anal plate triangular	Cerococcidae	p. 326

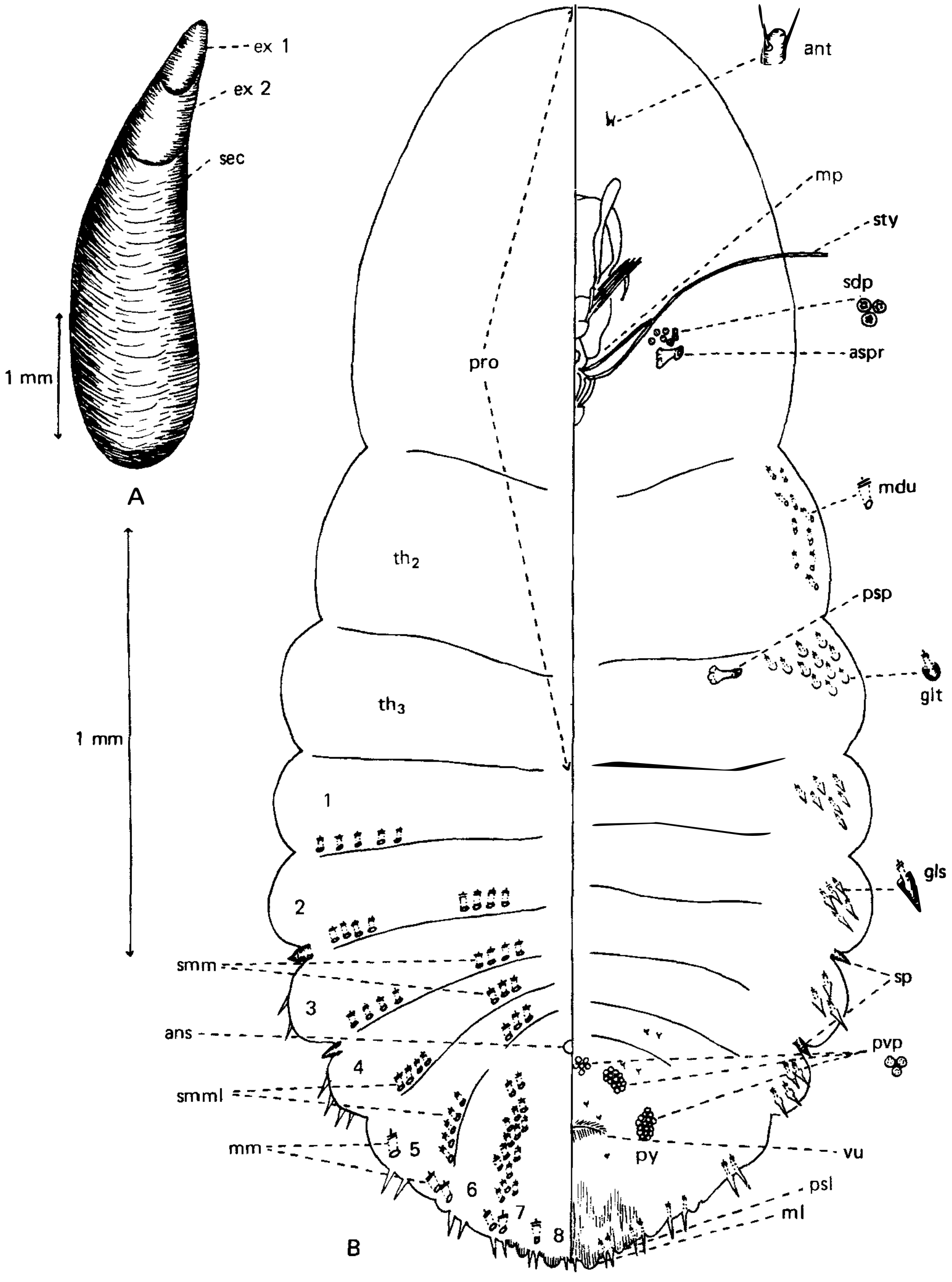


Figure 22–16 Morphological characters of armored scale insects (Diaspididae). A, scale of female; B, diagrammatic drawing of a female armored scale. The left side of B represents a dorsal view, and the right side a ventral view. *ans*, anus; *ant*, antenna; *aspr*, anterior spiracle; *ex 1*, first exuvium; *ex 2*, second exuvium; *gls*, gland spines; *glt*, gland tubercle; *mdu*, microduct; *ml*, median lobe; *mm*, marginal macroduct, *mp*, mouth parts; *pro*, prosoma; *psl*, paired second lobe; *psp*, posterior spiracle; *pvp*, perivulvar pores; *py*, pygidium; *sdp*, spiracular disc pore; *sec*, secretion of adult; *smm*, submedian macroduct; *smml*, submarginal macroducts; *sp*, spur; *sty*, stylets; *th_2*, mesothorax; *th_3*, metathorax; *vu*, vulva. (Figure prepared by Dr. Michael Kosztarab.)

95′.	Antennae 7- to 9-segmented, without an associated cluster of 5–7 locular pores; anal plate triangular, much wider than long	Lecanodiaspididae	p. 326
96(92′).	Locular pores usually in clusters, with common duct, scattered over dorsum; body with numerous, thick, truncate setae; on cacti	Dactylopiidae	p. 326
96′.	Pores not arranged as in preceding entry, setae usually not truncate; on various host plants	97	
97(96′).	Terminal abdominal segments fused to form pygidium (Figure 22–16, py); anal opening simple; body covered by thin, shieldlike scale	98	
97′.	Terminal abdominal segments not fused to form pygidium; anal opening often with setae; body not covered by thin, shieldlike scale	99	
98(97).	Beak and antennae 1-segmented; legs absent or vestigial; widely distributed	Diaspididae	p. 327
98′.	Beak 2-segmented, antennae 3- or 4-segmented; legs present and well developed; known from California and Florida	Conchaspididae	p. 327
99(97′).	Body surface with small irregularities; anal ring simple, with 0–2 setae and no pores; southwestern United States, on palms	Phoenicococcidae	p. 327
99′.	Body surface without small irregularities; anal ring variable; widely distributed, on various host plants	100	
100(99′).	Dorsal ostioles and usually 1–4 ventral circuli present (Figure 22–15B, do and vc); in life covered with white, powdery secretion	Pseudococcidae	p. 325
100′.	Dorsal ostioles and ventral circuli absent; in life usually naked, not covered with whitish, powdery secretion	101	
101(100′).	Usually with protruding anal lobes; anal ring usually with pores and setae; host plants varied	Eriococcidae	p. 326
101′.	Without protruding anal lobes; anal ring simple, without pores and setae; on oaks	Kermesidae	p. 326

INFRAORDER Enicocephalomorpha: The infraorder Enicocephalomorpha was formerly thought to be related to the Reduviidae because of similarities in head structure. Entomologists now believe it is different enough from other Hemiptera to constitute a separate suborder and probably represents the sister group of the rest of the order.

Family **Aenictopecheidae:** This is a rare family containing only two species, including a single American species, *Boreostolus americanus* Wygodzinsky and Štys. This species lives under large, flat stones and sandy substrates along mountain streams in Oregon, Washington, and Colorado. It is 5 mm long and occurs in both the macropterous and brachypterous condition. It is presumed to be predaceous.

Family **Enicocephalidae—Unique-Headed Bugs or Gnat Bugs:** These are small (2–5 mm long), slender, predaceous bugs that have a peculiarly shaped head and the front wings are entirely membranous (Figure 22–17). They usually live under stones or bark or in debris,

Figure 22–17 A gnat bug, *Systelloderes biceps* (Say), 15×. (Courtesy of Froeschner and The American Midland Naturalist.)

where they feed on various small insects. Some species form large swarms and fly about like gnats or midges. It is primarily a tropical group. Six genera and 11 species are known to occur in North America, 10 of which species are southwestern and western. One species is found in the Florida Keys.

INFRAORDER Dipsocoromorpha: The infraorder Dipsocoromorpha contains a few small and seldom-encountered bugs whose position in the order is not well understood.

***Family* Ceratocombidae:** These are tiny insects (2 mm long), with long, slender antennae and a distinct cuneal fracture. Two genera and four species are known from North America.

***Family* Dipsocoridae:** This is a family of primarily small tropical insects. They are elongate and flattened and only 2–3 mm long. The head is porrect. The labium does not exceed the fore coxae, and a distinct metapleural evaporatorium is present. The abdominal venter is densely pilose and the male genitalia strongly asymmetrical (sinistral). In North America only one genus (*Cryptostemma*), with two species, occurs. They live in moist habitats near clear streams, often under stones.

***Family* Schizopteridae:** These tiny (0.8–2 mm), beetlelike hemipterans are usually black with coleopteroid (beetlelike) wings, and no elongate hairs on the body. They are abundant in the tropics, but only four genera and four species are known from North America. They live chiefly in ground litter in moist areas.

INFRAORDER Nepomorpha: The Nepomorpha are aquatic (rarely shore-inhabiting). The antennae are shorter than the head and usually concealed in grooves on the underside of the head. Trichobothria are absent.

***Family* Nepidae—Waterscorpions:** The waterscorpions are predaceous aquatic bugs with raptorial front legs and with a long caudal breathing tube formed by the cerci. The breathing tube is often almost as long as the body and is thrust up to the surface as the insect crawls about on aquatic vegetation. These insects move slowly and prey on various types of small aquatic animals, which they capture with their front legs. Waterscorpions can inflict a painful bite when handled. They have well-developed wings but seldom fly. The eggs are inserted on or into the tissues of aquatic plants or into the substrate near the waterline.

Three genera and 12 species of waterscorpions occur in the United States and Canada. The nine species of *Ranatra* are slender and elongate with very long legs and are somewhat similar to walkingsticks in appearance (Figure 22–18B). The only North American species of *Nepa*, *N. apiculata* Uhler, has the body oval and somewhat flattened (Figure 22–18A). The body shape in *Curicta* is somewhat intermediate between those of *Ranatra* and *Nepa*. The most common North American waterscorpions belong to the genus *Ranatra*; *N. apiculata* is less common and occurs in the eastern states; the two species of *Curicta* are relatively rare and live in the Southwest.

***Family* Belostomatidae—Giant Water Bugs:** This family contains the largest bugs in the order, some of which (in the United States) may reach a length of 65 mm. One species in South America is more than 100 mm long. These bugs are elongate-oval and somewhat flattened, with raptorial front legs (Figure 22–19). They are fairly common in ponds and lakes, where they feed on other insects, snails, tadpoles, and even small fish. They frequently leave the water and fly about, and because they

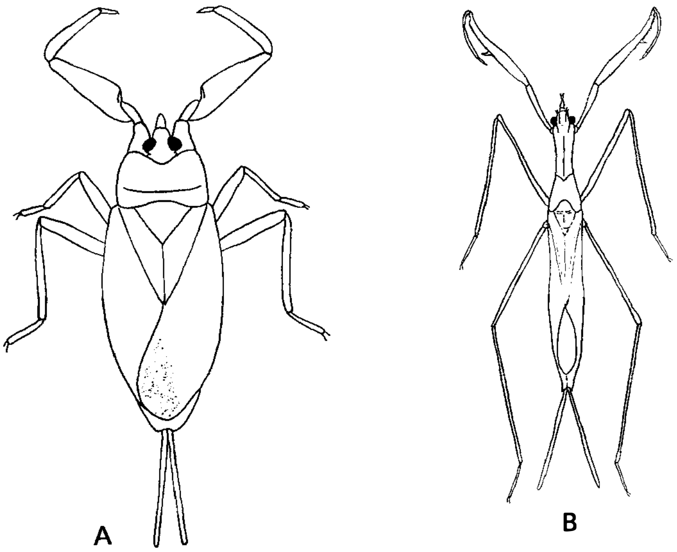


Figure 22–18 Waterscorpions. A, *Nepa apiculata* Uhler, 2×; B, *Ranatra fusca* Palisot de Beauvois, about natural size.

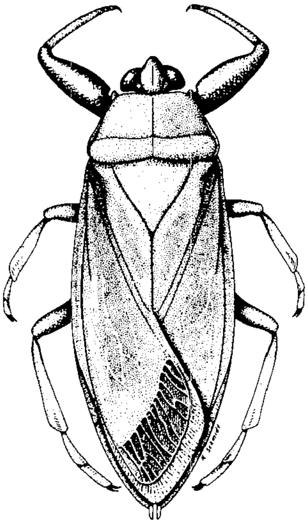


Figure 22–19 A giant water bug, *Lethocerus griseus* (Say), about natural size.

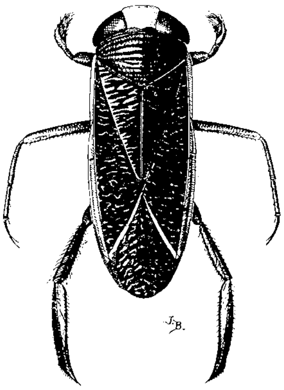


Figure 22–20 A water boatman, *Hesperocorixa atopodonta* (Hungerford) 7×. (Courtesy of Slater and Baranowski and the Wm. C. Brown Co.)

are often attracted to lights, they are sometimes called "electric light bugs." Giant water bugs can inflict a painful bite if handled carelessly. In some species (*Belostoma* and *Abedus*), the female lays her eggs on the back of the male, which then carries them about until they hatch. The eggs of other species (*Lethocerus*) are attached to aquatic vegetation.

The 19 species of giant water bugs in North America are classified in three genera: *Lethocerus*, *Belostoma*, and *Abedus*. The first two are widely distributed, whereas *Abedus* occurs only in the South and West. The species of *Lethocerus* are our largest belostomatids (45–65 mm long) (Figure 22–19) and have a very short basal segment of the beak. Most species of *Belostoma* are about 25 mm long, and they have a well-developed membrane of the hemelytra. *Abedus* has a much reduced membrane of the hemelytra. One species occurring in the Southwest (usually in streams) is 27–37 mm long, but a relatively rare species in the southeastern states is only 12–15 mm long.

***Family* Corixidae—Water Boatmen:** This is the largest family in the infraorder, with about 120 North American species, and its members are common in freshwater ponds and lakes. They occasionally occur in streams, and a few species live in the brackish pools just above the high-tide mark along the seashore. The body is elongate-oval (Figure 22–20), somewhat flattened, and usually dark gray. The dorsal surface of the body is often cross-lined. The middle and hind legs are elongate, and the hind legs are oarlike. The beak is broad, conical, and unsegmented; the front wings are uniform in texture throughout; and the front tarsi are scoop-shaped (Figure 22–6B). Like all other aquatic bugs, they lack gills and get air at the surface of the water. They frequently carry a bubble of air under water, either on the surface of the body or under the wings. They swim rapidly, usually in a somewhat erratic fashion, and often cling to vegetation for long periods.

Most water boatmen feed on algae and other minute aquatic organisms. A few are predaceous, feeding on midge larvae and other small aquatic animals. They can apparently take in solid particles of food, not just liquids.

The eggs of water boatmen are usually attached to aquatic plants. In some parts of the world (for example, certain parts of Mexico), people use water boatmen eggs as food. They collect the eggs from aquatic plants, dry them, and later grind them into flour. Water boatmen are an important item of food for many aquatic animals.

***Family* Ochteridae—Velvety Shore Bugs:** These oval-bodied insects, 4–5 mm long, live along the shores of quiet streams and ponds, but they are uncommon. They are velvety bluish or black and are predaceous. Seven species occur in the United States.

***Family* Gelastocoridae—Toad Bugs:** These bugs superficially resemble small toads, in both appearance and hopping habits. They are short and broad, have large projecting eyes (Figure 22–21), and are usually found along the moist margins of ponds and streams. Toad bugs capture their prey (other insects) by grasping it in their front legs. The eggs are laid in sand. Many species can change colors depending on the color of the substrate. This family is a small one, with only seven species in North America.

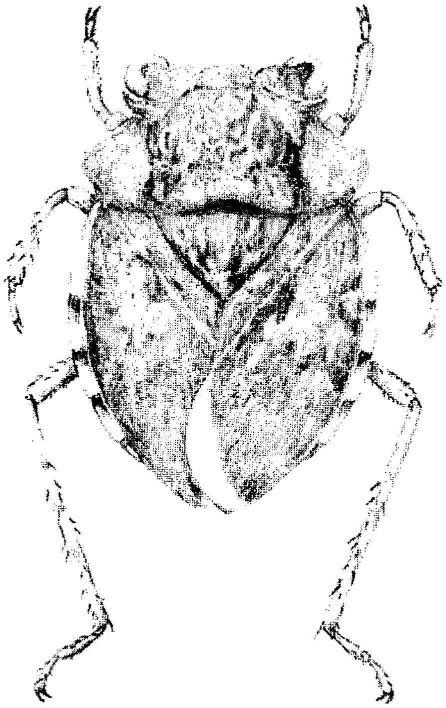


Figure 22–21 A toad bug, *Gelastocoris oculatus* (Fabricius). 7½×.

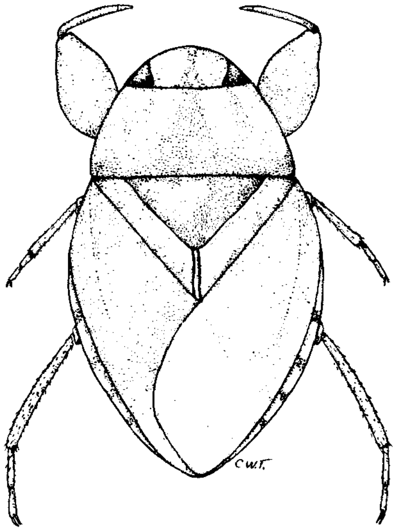


Figure 22–22 A creeping water bug, *Pelocoris femoratus* (Palisot de Beauvois), 5×.

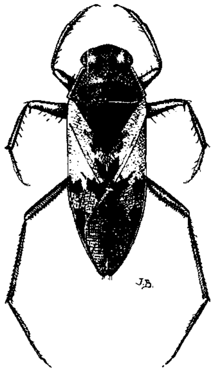


Figure 22–23 A backswimmer, *Notonecta insulata* Kirby, 4×. (Courtesy of Slater and Baranowski and the Wm. C Brown Co.)

Family **Naucoridae—Creeping Water Bugs:** These bugs are brownish, broadly oval and somewhat flattened, and 9–13 mm long. The front femora are greatly thickened (Figure 22–22). They are most common in quiet water, where they may be found on submerged vegetation or in debris. Some occur in streams. They feed on various small aquatic animals. They bite quite readily—and painfully—when handled. There are about 20 North American species, only two of which (in the genus *Pelocoris*) occur in the East.

Family **Notonectidae—Backswimmers:** The backswimmers are so named because they swim upside down. They are very similar to the water boatmen in shape (Figure 22–23), but have the dorsal side of the body more convex and usually light-colored. They frequently rest at the surface of the water, with the body at an angle and the head down, and with the long hind legs extended. They can swim rapidly, using the hind legs like oars.

Backswimmers are predaceous, feeding on other insects and occasionally on tadpoles and small fish. They frequently attack animals larger than themselves and feed by sucking the body fluids from their prey. A common method of capturing prey is to drift up under it after releasing hold of a submerged plant to which the attacker has been clinging. These insects will bite people when handled, and the effect is much like a bee sting. Backswimmer eggs are deposited in the tissues of aquatic plants or glued to the surface of a plant.

Males of many species of backswimmers stridulate during courtship, by rubbing the front legs against the beak. The structure of the stridulatory areas often provides characters of value in separating species.

There are 34 species of backswimmers in North America, in three genera: *Buenoa*, *Notonecta*, and *Martarega*. The species of *Buenoa* are small (5–9 mm long) and slender, with the antennae three-segmented, the hemelytra glabrous, and the scutellum distinctly shorter than the claval commissure. The other two genera are usually larger (8–17 mm long) and a little stouter. The antennae are four-segmented, and the hemelytra are usually longer than the claval commissure. Most of the species, and most specimens collected, belong to the genus *Notonecta.*

***Family* Pleidae—Pygmy Backswimmers:** These bugs are similar to the Notonectidae, but are very small (1.6–2.3 mm long) and have a very convex dorsal surface of the body, with the wings forming a hard shell. Seven species occur in North America.

INFRAORDER Gerromorpha: The members of this group are semiaquatic or shore-inhabiting; they have conspicuous antennae; and have three pairs of trichobothria on the head.

***Family* Mesoveliidae—Water Treaders:** These bugs are usually found crawling over floating vegetation at the margins of ponds or pools or on logs projecting from the water. When disturbed, they run rapidly over the surface of the water. They are small (5 mm long or less), slender, and usually greenish or yellowish green (Figure 22–24A). Within a species, some adults are winged and some are wingless. These insects feed on small aquatic organisms on and just beneath the surface of the water.

***Family* Hydrometridae—Water Measurers or Marsh Treaders:** These bugs are small (about 8 mm long), usually grayish, and very slender. They resemble tiny walkingsticks (Figure 22–25). The head is very long and slender, with the eyes conspicuously bulging laterally. These insects are usually wingless. They occur in shallow water among vegetation and feed on minute organisms. They frequently walk very slowly over surface vegetation or over the surface of the water. The eggs, which are elongate and about one-fourth as long as the adult, are laid singly and glued to objects near the water. Only seven species, all belonging to the genus *Hydrometra*, occur in North America.

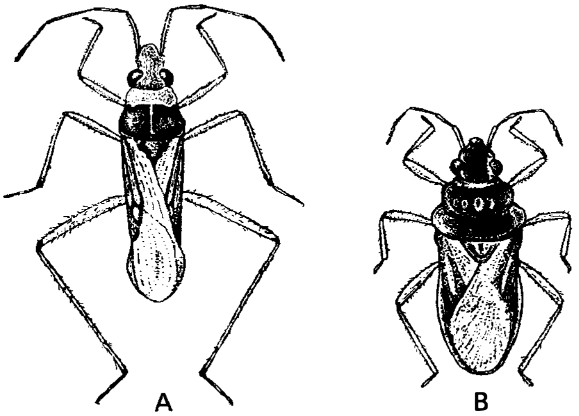


Figure 22–24 A, a water treader, *Mesovelia mulsanti* White, 9×; B, a velvet water bug, *Hebrus sobrinus* Uhler, 16×. (Courtesy of Froeschner and The American Midland Naturalist.)

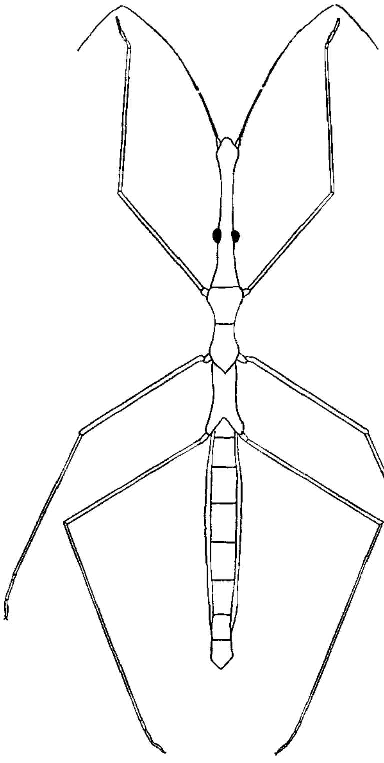


Figure 22–25 A water measurer, *Hydrometra martini* Kirkaldy, 7½×.

***Family* Hebridae—Velvet Water Bugs:** The hebrids are small (less than 3 mm long), oblong bugs with a broad-shouldered appearance (Figure 22–24B), and the entire body is covered with velvety hairs. They occur on the surface of shallow pools where there is an abundance of aquatic vegetation and in damp soil near the water's edge. They are believed to be predaceous. This group contains 15 North American species, in two genera: *Merragata* (antennae four-segmented) and *Hebrus* (antennae five-segmented).

***Family* Macroveliidae:** This group is represented in North America by two species in two genera in the western states. *Macrovelia hornii* Uhler resembles a mesoveliid in appearance (see Figure 22–24A), but differs in having six closed cells in the hemelytra, and the pronotum has a backward-projecting lobe that covers the scutellum. It lives along the shores of springs and streams, usually in moss or other protected places. It does not run about on the water surface, but it has never been taken more than a few feet from the water's edge.

Family **Veliidae—Broad-Shouldered Water Striders, Riffle Bugs**: These water striders are small (1.6–5.5 mm long) and brown or black, often with silvery markings. They are usually wingless. They live on the surface of the water or on the adjacent shore and feed on various small insects. Members of the genus *Rhagovelia* (Figure 22–26B) are gregarious, and a single sweep of a dip net may sometimes yield up to 50 or more specimens. These veliids live on or near the riffles of small streams, but members of other genera are usually inhabit quieter parts of streams or on ponds. Three widely distributed genera, with more than 30 species, occur in the United States: *Rhagovelia*, *Microvelia*, and *Paravelia*.

Family **Gerridae—Water Striders**: The water striders are long-legged insects (Figure 22–26A) that live on the surface of the water, running or skating over the surface and feeding on insects that fall onto the water. The front legs are short and are used in capturing food; the middle and hind legs are long and are used in locomotion. Most species are black or dark-colored, and the body is long and narrow.

The tarsi of water striders are clothed with fine hairs and are difficult to wet. This tarsal structure enables a water strider to skate around on the surface of the water. If the tarsi become wet, the insect can no longer stay on the surface film; it will drown unless it can crawl up on some dry surface. When the tarsi dry again, they function normally.

These insects are common on quiet water in small coves or protected places. They often live together in large numbers. Species inhabiting small intermittent streams burrow down in the mud or under stones when the stream dries up and remain dormant until the stream fills with water again. The adults hibernate in such situations. Except for one genus, the water striders are restricted to fresh water. The species in the genus *Halobates* live on the surface of the ocean, often many miles from land. Winged and wingless adults occur in many species, and the insect moves from one aquatic situation to another when in the winged stage. The eggs are laid at the surface of the water on floating objects.

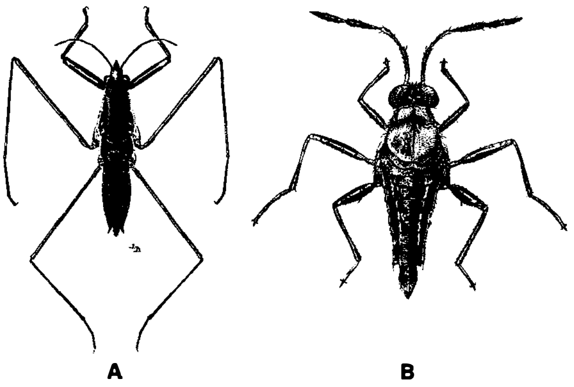


Figure 22–26 Water striders. **A**, *Gerris* sp. (Gerridae), 5×; **B**, *Rhagovelia obesa* Uhler (Veliidae), 10×. (Courtesy of Slater and Baranowski and the Wm. C Brown Co.)

INFRAORDER Leptopodomorpha

Family **Saldidae—Shore Bugs**: The shore bugs are small, oval, flattened, usually brown or black-and-white bugs that are often common along shores of streams, ponds, or the ocean. Some are burrowing in habit. When disturbed, they fly quickly for a short distance and then scurry under vegetation or into a crevice. They are predaceous on other insects. The shore bugs can usually be recognized by the four or five long, closed cells in the membrane of the hemelytra (Figure 22–4F). There are about 70 North American species of shore bugs.

Family **Leptopodidae—Spiny Shore Bugs**: This is an Old World group, one species of which, *Patapius spinosus* (Rossi), has been introduced into California. It may be found from Butte County south to Los Angeles County. This spiny bug is 3.3 mm long and is yellowish brown with two dark brown transverse bands on the hemelytra.

INFRAORDERS Cimicomorpha and Pentatomomorpha: These bugs are all terrestrial; they almost always have conspicuous antennae; and they usually have trichobothria. The majority are plant feeders, feeding on sap, flowers, fruits, or even mature seeds, but many taxa are predaceous.

INFRAORDER Cimicomorpha

Family **Thaumastocoridae—Royal Palm Bugs**: This group is represented in the United States by a single species, *Xylastodoris luteolus* Barber, which occurs in Florida. This insect is 2.0–2.5 mm long, flattened, oblong-oval, and pale yellowish with reddish eyes. It feeds on the royal palm.

Family **Tingidae—Lace Bugs**: This is a fairly large group (about 140 North American species) of small (shorter than 5 mm) bugs that have the dorsal surface of the body rather elaborately sculptured (Figure 22–27). This lacelike appearance is found only in the adults; the nymphs are usually spiny. These bugs are plant feeders, and whereas most species feed on herbaceous plants, some of our most common species feed on trees. Their feeding causes a yellow spotting of the leaf, and with continued feeding the leaf becomes entirely brown and falls off. Some species do considerable damage to trees.

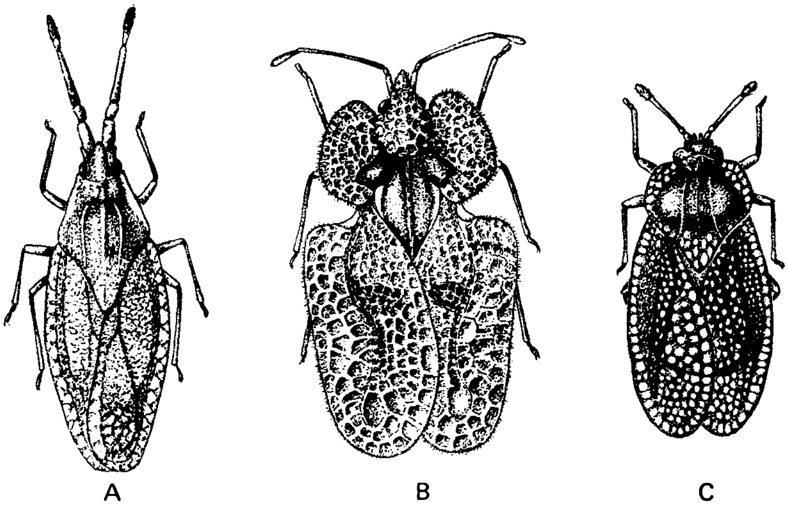


Figure 22–27 Lace bugs. A, *Atheas mimeticus* Heidemann, 18×; B, the sycamore lace bug, *Corythuca ciliata* (Say), 13×; C, *Acalypta lillianis* Bueno, 14×. (A and B redrawn from Froeschner and the American Midland Naturalist; C, redrawn from Osborn and Drake and the Ohio Biological Survey).

The eggs are usually laid on the underside of the leaves. *Corythuca ciliata* (Say) (Figure 22–27B), a common species that is somewhat milky in color, feeds chiefly on sycamore.

Family **Microphysidae:** This family is represented in the United States by four species in four genera. One species, *Mallochiola gagates* (McAtee and Malloch), resembles a mirid in having a cuneus, but it has ocelli, symmetrical male genitalia, and the tarsi are two-segmented; it is broadly oval and somewhat flattened, shining black, and 1.2 mm long. It is known only from Maryland and the District of Columbia.

Family **Miridae—Plant Bugs or Leaf Bugs:** This is the largest family in the order (about 1750 North American species), and its members are to be found on vegetation almost everywhere. Some are very abundant. Most species are plant feeders, but many are predaceous on other insects. Some of the plant-feeding species are pests of cultivated plants.

The mirids are soft-bodied bugs, mostly 4–10 mm long, that may be variously colored. Some species are brightly marked with red, orange, green, or white. Members of this group can be recognized by the presence of a cuneus and only one or two closed cells at the base of the membrane (Figure 22–1 and 22–4A). The antennae and beak are four-segmented; the ocelli are lacking (except for the Isometopinae).

Figure 22–28 illustrates some of the more important mirids that attack cultivated plants. The meadow plant bug, *Leptopterna dolobrata* (L.) (Figure 22–28D), is abundant in meadows and pastures in early summer and does considerable damage to grass. It is 7–9 mm long. The tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) (Figure 22–28C), is brown with a Y-shaped mark on the scutellum. It is a very common bug and often seriously damages legumes, vegetables, and flowers. This species occurs throughout the eastern and central states. Other species of *Lygus* are serious crop pests in the West. The four-lined plant bug, *Poecilocapsus lineatus* (Fabricius) (Figure 22–28E), is yellowish or greenish with four longitudinal black stripes on the body. It feeds on a large number of plants and sometimes causes serious damage to currants, gooseberries, and some ornamental flowers. The apple red bug, *Lygidea mendax* Reuter (Figure 22–28B), a red and black bug about 6 mm long, was at one time a serious pest of apples in the Northeast, but has become less important in recent years. The rapid plant bug, *Adelphocoris rapidus* (Say) (Figure 22–28F), is 7–8 mm long and dark brown with yellowish margins on the front wings. It feeds chiefly on dock, but sometimes injures cotton and legumes. The garden fleahopper, *Halticus bractatus* (Say) (Figure 22–28A), is a common leaf bug that is often brachypterous. It is a shining black, jumping bug, 1.5–2.0 mm long, that feeds on many cultivated plants but is often a pest of legumes. The front wings of the female (the sex illustrated) lack a membrane and resemble the elytra of a beetle. The males have normal wings, but the membrane is short.

This family is divided into a number of subfamilies, one of which, the Isometopinae, is sometimes given family rank. These mirids, commonly called "jumping ground bugs," differ from other mirids in having ocelli. They are found on bark and dead twigs, and they jump quickly when disturbed. The group is a small one, with less than a dozen North American species, all relatively rare.

Family **Nabidae—Damsel Bugs:** The nabids are small bugs (3.5–11.0 mm long) that are relatively slender with the front femora slightly enlarged (Figure 22–29), and the membrane of the hemelytra (when developed) has a number of small cells around the

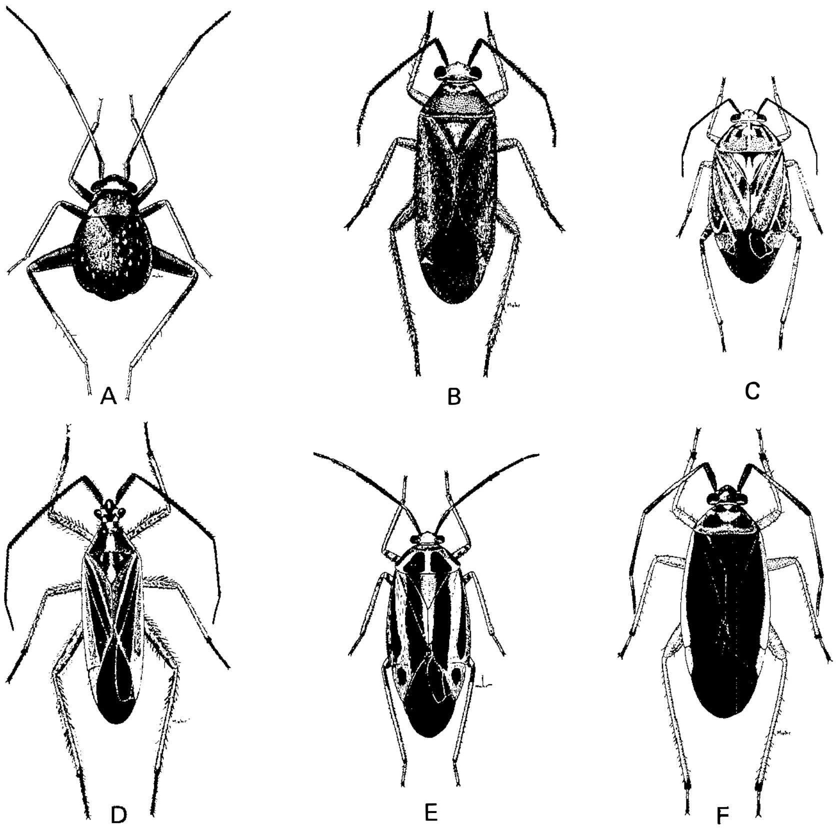


Figure 22–28 Plant or leaf bugs (Miridae). A, garden fleahopper, *Halticus bractatus* (Say), female, 10×; B, apple red bug, *Lygidea mendax* Reuter, female, 5×; C, tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), 4×; D, meadow plant bug, *Leptopterna dolobrata* (L.), male 4×; E, four-lined plant bug, *Poecilocapsus lineatus* (Fabricius), 4×; F, rapid plant bug, *Adelphocoris rapidus* (Say), 4×. (Redrawn from the Illinois Natural History Survey.)

margin (Figures 22–4E and 22–29A). These bugs are predaceous on many different types of insects, including aphids and caterpillars.

The most commonly encountered damsel bugs are pale yellowish to brownish with well-developed wings. *Nabis americoferus* Carayon (Figure 22–29A) is common throughout the United States. Some of the nabids occur in both long-winged and short-winged forms, but the long-winged forms are in many cases quite rare and it is the short-winged forms that are usually encountered. A fairly common nabid of this sort is *Nabicula subcoleoptrata* (Kirby), a shining black insect (Figure 22–29B) usually found in meadows, where it feeds chiefly on the meadow plant bug, *Leptopterna dolobrata.*

Family **Lasiochilidae**: These bugs have the general habitus of Anthocoridae but not the asymmetrical male genitalia, and insemination occurs in the vagina of the female. Our species are 3–4 mm long. The presence of dorsal lateral tergites on abdominal segments one and two appears to be diagnostic. Most species have been reported to live under bark. More than 30 species are

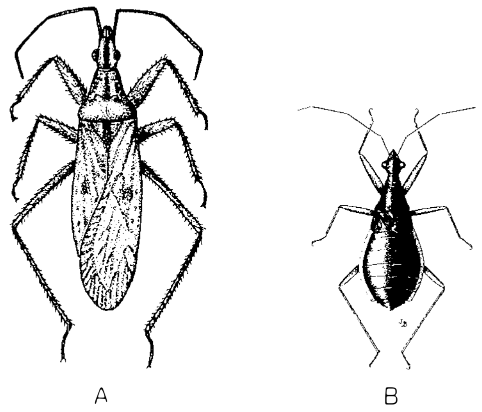


Figure 22–29 Damsel bugs. A, *Nabis americoferus* Carayon, 5×; B, *Nabicula subcoleoptrata* (Kirby), 4×. (A, redrawn from Froeschner and the American Midland Naturalist; B, courtesy of Slater and Baranowski and the Wm. C Brown Co.)

known to occur in North America, most of them southwestern and western.

Family **Lyctocoridae:** Although similar in general appearance to Anthocoridae, the species of this family differ in the type of asymmetrical male genitalia with both parameres developed and the aedeagus does not "ride" in a groove in the left paramere. A difficult, but definitive character is the presence of apophyses on the anterior margin of abdominal sternum 7. About 36 species occur in North America. Of these the best known is *Lyctocoris campestris* (Fabricius), which is common and widely distributed. It may be an introduced species and sometimes is known to live in nests of rodents and to suck blood of domestic animals and humans.

Family **Anthocoridae—Minute Pirate Bugs:** This family formerly included the Lyctocoridae and Lasochilidae. As presently restricted, it contains small, flattened bugs 2–5 mm long, elongate, with the male genitalia asymmetrical and with a sickle-shaped paramere; many species are black with whitish markings (Figure 22–30B). Although sometimes found on the ground and under bark, many species occur on flowers and fruits. Most species are predaceous, feeding on various small insects and insect eggs. The insidious flower bug, *Orius insidiosus* (Say) (Figure 22–30B), is an important predator on the eggs and larvae of the corn earworm and many other pests. The bite of this bug is surprisingly painful for such a tiny insect. The common species of anthocorids are usually found on flowers, but some species live under loose bark, in leaf litter, and in decaying fungi. About 43 species occur in North America.

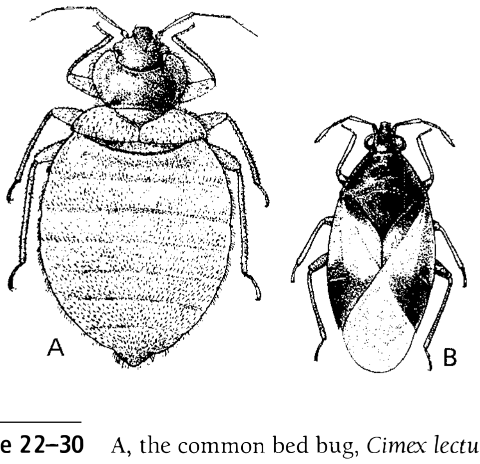


Figure 22–30 A, the common bed bug, *Cimex lectularius* (L.), 7×; B, the insidious flower bug, *Orius insidiosus* (Say), 16×. (Courtesy of Froeschner and The American Midland Naturalist.)

Family **Cimicidae—Bed Bugs:** The bed bugs are flat, broadly oval, wingless bugs about 6 mm long (Figure 22–30A) that feed by sucking blood from birds and mammals. The group is a small one, but some of the species are widely distributed and well known. The common bed bug that attacks people is *Cimex lectularius* L. This species is sometimes a pest in houses, hotels, barracks, and other living quarters. It also attacks animals other than humans. A tropical species, *Cimex hemipterus* (Fabricius) also bites people. Other species in this family attack bats and various birds.

The common bed bug is largely nocturnal and, during the day, hides in cracks in a wall, under the baseboard, in the springs of a bed, under the edge of a mattress, under wallpaper, and in similar places. Its flatness makes it possible for it to hide in very small crevices. Bed bugs may be transported from place to place on clothing or in luggage or furniture, or they may migrate from house to house. They lay their eggs, 100–250 per female, in cracks. Development to the adult stage requires about 2 months in warm weather. The adults may live for several months and can survive long periods without food. Bed bugs are important primarily because of their irritating bites; they are apparently unimportant as disease vectors.

Family **Polyctenidae—Bat Bugs:** Only two rare species of bat bugs occur in the United States, one in Texas and the other in California. They are ectoparasites of bats. These bugs are wingless and lack compound eyes and ocelli. The front legs are short and flattened, and the middle and hind legs are long and slender. The body is generally covered with bristles. These bugs are 3.5 to 4.5 mm long.

Family **Reduviidae—Assassin Bugs, Ambush Bugs, and Thread-Legged Bugs:** This is a large group (more than 160 North American species) of predaceous bugs, and many species are fairly common. They are often blackish or brownish, but many are brightly colored. The head is usually elongate, with the area behind the eyes constricted and necklike. The beak is short and three-segmented, and its tip fits into a stridulatory groove in the prosternum (Figure 22–7B). The abdomen in many species is widened in the middle, exposing the lateral margins of the segments beyond the the wings. Most species are predaceous on other insects, but a few are bloodsucking and frequently bite people. Many species inflict a painful bite if carelessly handled.

One of the largest and most easily recognized assassin bugs is the wheel bug, *Arilus cristatus* (L.), a grayish bug 28–36 mm long, with a semicircular crest on the pronotum that terminates in teeth and resembles a cogwheel (Figure 22–31B). This species is fairly common in the East. The masked hunter, *Reduvius personatus* (L.), is a brownish black bug (it resembles the reduviid shown in Figure 22–31C), 17–22 mm long, that is often found in houses. It feeds on bed bugs, but it will also bite people. The nymphs are soft-bodied and cover themselves with dust particles; they are often called "dust bugs" or "masked bedbug hunters."

The assassin bugs in the genus *Triatoma* also invade houses and bite people. They feed at night, biting any exposed parts (such as the face) of people sleeping. These bugs are sometimes called "kissing bugs" (because of their tendency to bite people about the mouth) or "Mexican bed bugs." In South America, species of this genus serve as vectors of a trypanosome disease of humans known as Chagas disease (several cases of this disease have recently been reported in the United States). Armadillos, opossums, and certain rats also serve as a host for the trypanosome causing this disease.

Ambush bugs (Phymatinae) are small, stout-bodied bugs with the front femora much thickened and the terminal antennal segment swollen (Figure 22–31F). Most of the ambush bugs are about 13 mm long or less, yet they can capture insects as large as fair-sized bumble bees. They lie in wait for their prey on flowers, particularly goldenrod, where they are excellently con-

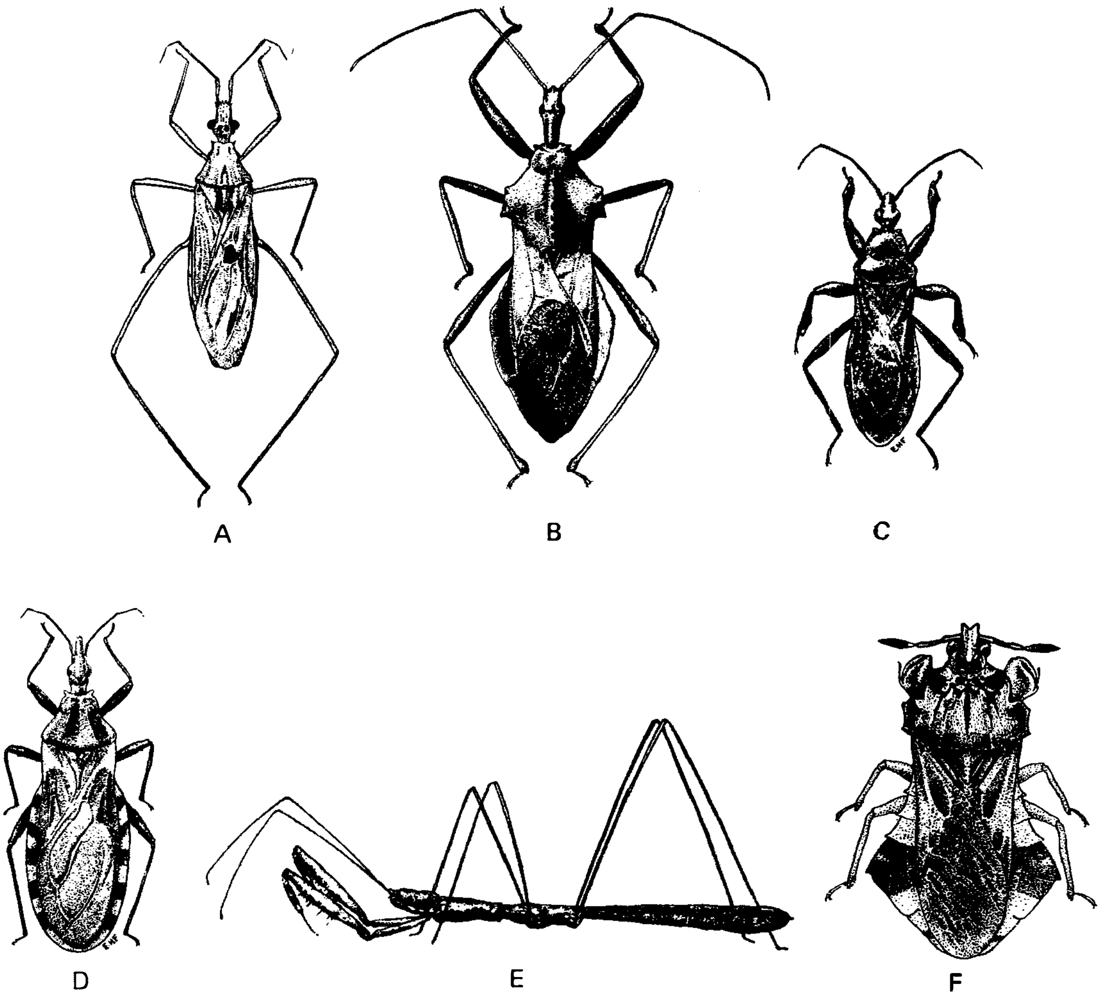


Figure 22–31 Assassin bugs (A–D), a thread-legged bug (E), and an ambush bug (F). A, *Narvesus carolinensis* Stål, 2½×; B, the wheel bug, *Arilus cristatus* (L.) 1½×; C, *Melanolestes picipes* (Herrick-Schäffer), 2×; D, a blood-sucking conenose, *Triatoma sanguisuga* (LeConte), 2×; E, *Barce uhleri* (Banks), 5½×; F, *Phymata fasciata georgiensis* Melin, 4½×. (Courtesy of Froeschner and The American Midland Naturalist.)

cealed by their greenish yellow color. They feed principally on large bees, wasps, and flies.

The thread-legged bugs (Emesinae) are very slender and long-legged and resemble walkingsticks (Figure 22–31E). They live in old barns, cellars, and dwellings, and outdoors beneath loose bark and in grass tufts, where they catch and feed on other insects. One of the largest and most common of the thread-legged bugs is *Emesaya brevipennis* (Say), a widely distributed species that is 33–37 mm long. Most of the thread-legged bugs are smaller (down to 4.5 mm long). *Barce uhleri* (Banks) (Figure 22–31E) is 7–10 mm long.

Family **Aradidae—Flat Bugs:** Nearly a hundred species in this group occur in North America. They are 3–11 mm long, usually dark brownish, very flat bugs (Figure 22–32), with the body surface somewhat granular. The wings are well developed but small and do not cover the entire abdomen. The antennae and beak are four-segmented (sometimes only two to three segments of the beak are visible); the tarsi have two segments; and there are no ocelli. These insects are usually found under loose bark or in crevices of dead or decaying trees. They feed on fungi.

Family **Piesmatidae—Ash-Gray Leaf Bugs:** These small bugs (2.5–3.5 mm long) can usually be recognized by their reticulately sculptured corium and clavus, the two-segmented tarsi, the ridges of the pronotum, and the juga extending well beyond the tylus (Figure 22–33). They are plant feeders and are probably found most often on pigweed (*Amaranthus*), but also feed on other plants. The 10 North American species in this group belong to the genus *Piesma*.

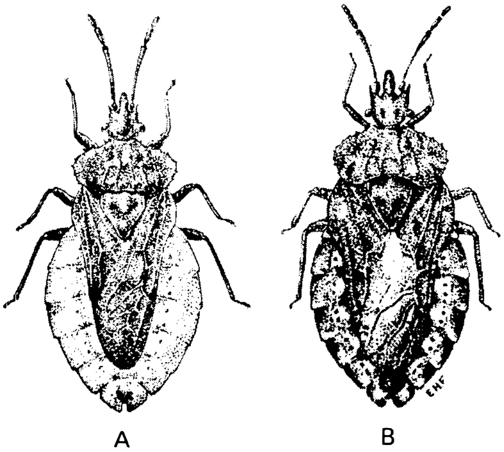


Figure 22–32 Flat bugs (Aradidae). A, *Aradus inornatus* Uhler, 4½×; B, *Aradus acutus* (Say), 5½×. (Redrawn from Froeschner and The American Midland Naturalist.)

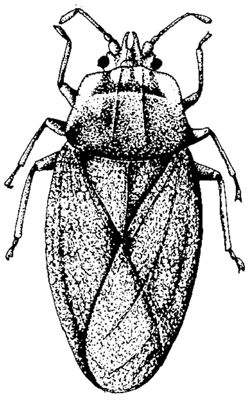


Figure 22–33 An ash-gray leaf bug, *Piesma cinerea* (Say), 15× (Redrawn from Froeschner and The American Midland Naturalist.)

Family **Berytidae—Stilt Bugs:** The stilt bugs are slender and elongate and have very long and slender legs and antennae (Figure 22–34). They resemble the water measurers (Figure 22–25) and thread-legged bugs (Figure 22–31E), but the head is not greatly elongate and they never live on the surface of the water (as do water measurers). In addition, they do not have raptorial front legs (as do the thread-legged bugs). They live on vegetation and feed chiefly on plants, although some species are partly predaceous. They are 5–9 mm long and usually brownish.

Family **Rhyparochromidae:** This is a large family of mostly dull-colored, ground living species with enlarged and spinose fore femora (Figure 22–35B, E, F).

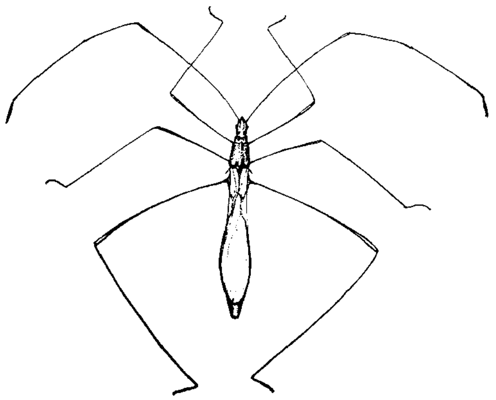


Figure 22–34 The spined stilt bug, *Jalysus wickhami* Van Duzee, 3½×. (Courtesy of Froeschner and The American Midland Naturalist.)

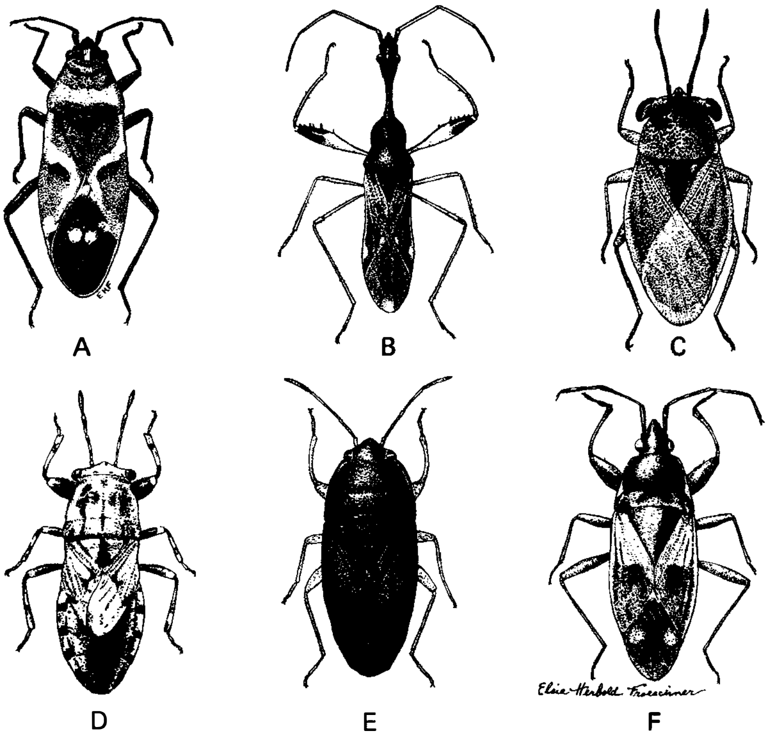


Figure 22–35 Lygaeoidea. A, the small milkweed bug, *Lygaeus kalmii* Stål, 3× (Lygaeidae); B, *Myodocha serripes* Olivier, 4× (Rhyparochromidae); C, a big-eyed bug, *Geocoris punctipes* (Say), 8× (Geocoridae); D, *Phlegyas abbreviatus* (Uhler), 8× (Pachygronthidae); E, *Aphanus illuminatus* (Distant), 6× (Rhyparochromidae); F, *Eremocoris ferus* (Say) (Rhyparochromidae). (Courtesy of Froeschner and The American Midland Naturalist.)

Despite the appearance of predatory habits because of their enlarged and spiny profemora, they feed on mature seeds. It is a large group, with about 165 species known to occur in North America. The incomplete, forward-curving abdominal suture between sterna 4 and 5 identifies them.

***Family* Lygaeidae—Seed Bugs:** Until recently, this was an omnibus family that is now divided into 10 separate families in North America. Now the family contains only the old subfamilies Lygaeinae, Orsillinae, and Ischnorthynchinae. It is readily recognizable by having all the abdominal spiracles dorsal. Many of the species are brightly colored orange and black or red and black, and many of these feed on milkweeds and other plants that are distasteful or toxic to other animals (Figure 22–35A). *Oncopeltus fasciatus* (Dallas) has been used extensively as an experimental laboratory animal and its flight patterns studied. Species feed chiefly, but not exclusively on seeds, and although a few are ground-living, the majority in North America tend to live aboveground, sometimes in trees. *Nysius ericae* Schilling and related species are often pests of cultivated crops. About 75 species are known to occur in North America.

***Family* Blissidae:** This family is characterized by having only the spiracles of abdominal segment 7 ventral and by lacking conspicuous punctures on the hemelytra. All known North American species breed only on monocot plants and are sap suckers rather than seed feeders. The chinch bug, *Blissus leucopterus* (Say) (Figure 22–36), is probably the most injurious bug in this family, attacking wheat, corn, and other cereals. Sometimes it becomes a serious pest of turf grasses. It is about 3.5 mm long and is black with white front wings. Each front wing has a black spot near the middle of the costal margin. Both long-winged and short-winged forms occur in this species (Figure 22–36C,D).

Chinch bugs overwinter as adults in grass clumps, fallen leaves, hedgerows and other protected places. They emerge about the middle of April and begin feeding on small grains. The eggs are laid during May, either in the ground or in grass stems near the ground, and hatch about a week or 10 days later. Each female may lay several hundred eggs. The nymphs feed on the juices of grasses and grains and reach maturity in 4 to 6 weeks. By the time these nymphs become adult, the small grains (wheat, rye, oats, and barley) are nearly mature and no longer succulent, and the adults (along with nymphs nearly adult) migrate to other fields of more succulent grain, usually corn. They migrate on foot, often in great numbers. The females lay eggs for a second generation on the corn, and this generation reaches maturity in late fall and then seeks out places of hibernation. When chinch bugs are abundant, they

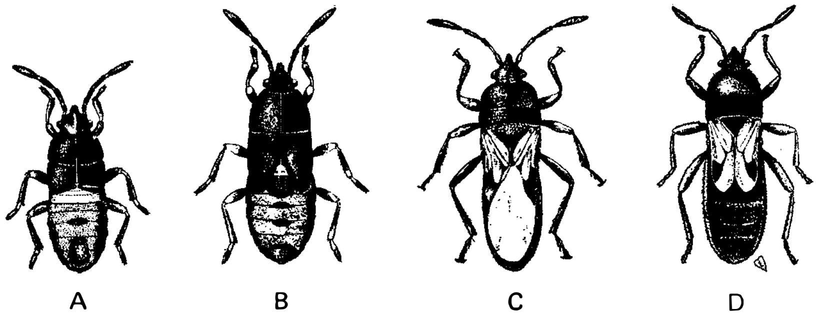


Figure 22–36 The chinch bug, *Blissus leucopterus* (Say). A, fourth instar nymph; B, fifth instar nymph; C, adult; D, short-winged adult. (Courtesy of USDA.)

may destroy whole fields of grain. A close relative of the chinch bug, *Blissus insularis* Barber, is a major pest of lawn grasses in the southeastern states. There are 29 species of blissids known from North America.

Family **Ninidae:** This is a small family readily recognized by the bifid apex of the scutellum, partially hyaline clavus, and peculiar two-stepped rostrum. Only a single species, *Cymoninus notabilis* (Distant), occurs in North America, where it is confined to the Gulf states from Florida to Texas. It breeds on a number of sedges.

Family **Cymidae:** These are small, dull yellow to straw-colored, coarsely punctate bugs that often resemble the seeds of the sedges and rushes on which they live. The nymphs are particularly cryptic. Ten species from North America are recognized at present.

Family **Geocoridae—Big-Eyed Bugs:** The members of this family are known as "big-eyed bugs" because of the large, reniform (kidney-shaped) eyes that protrude from the head and often curve back over the outer margins of the pronotum (Figure 22–35C). The dorsal position of the spiracles on abdominal segments 3 and 4 is diagnostic. North American species are short-bodied and for the most part live on or near the ground. Most are predaceous and have been used extensively in biological control studies. However, they are, in part at least, also plant feeders. Approximately 27 species occur in North America.

Family **Artheneidae:** This is a small family of somewhat flattened, yellowish to straw-colored bugs, readily recognizable by the broadly explanate margins of the pronotum. This family is not native to North America, but two Palearctic species, *Chilacis typhae* (Perris) and *Holcocranum saturejae* (Kolenati), have successfully established themselves. They breed on the catkins of cattails.

Family **Oxycarenidae:** Members of this family lack the explanate margins of the pronotum found in the Artheneidae, but share with them the dorsal position of the spiracles of abdominal segment 2. In the Old World tropics, some members of this family are pests of cotton and other crops. One of these is established in the American tropics but has not yet reached North America. Ten species occur at present in North America, nine of them western, where several live in the cones of conifers.

Family **Pachygronthidae:** Members of this family are readily recognizable by having all the abdominal spiracles ventral, being coarsely punctate, and with strongly incrassate and spinose fore femora (Figure 22–35D). Seven species occur in North America. One genus (*Phlegyas*) is widespread on grasses, the others (*Oedancala*) are sedge and rush feeders.

Family **Heterogastridae:** This family is recognizable by the ventral abdominal spiracles and the presence of a large, closed cell at the base of the membrane of the front wing. They are dull-colored, rather bulky insects and feed on urticaceous and related plants. Only two species, both western, occur in North America.

Family **Largidae:** These bugs are similar to the pyrrhocorids in appearance and habits (Figure 22–37A,B). Some of them, such as *Arhaphe carolina* (Herrich-Shäffer), are very antlike in appearance and have short hemelytra (Figure 22–37A). These bugs occur principally in the southern states.

Family **Pyrrhocoridae—Red Bugs and Cotton Stainers:** These are medium-sized (11–17 mm long), elongate-oval bugs that are usually brightly marked with red or brown and black. They resemble large lygaeids, but lack ocelli and have many branched veins and cells in the membrane of the hemelytra (as in Figure 22–4H). An important pest species in this family is the cotton stainer, *Dysdercus suturellus* (Herrich-Schäffer) (Figure 22–37C), which is a serious pest of cotton in some parts of the South. In feeding it stains the cotton fibers and greatly reduces their value. This family is a small

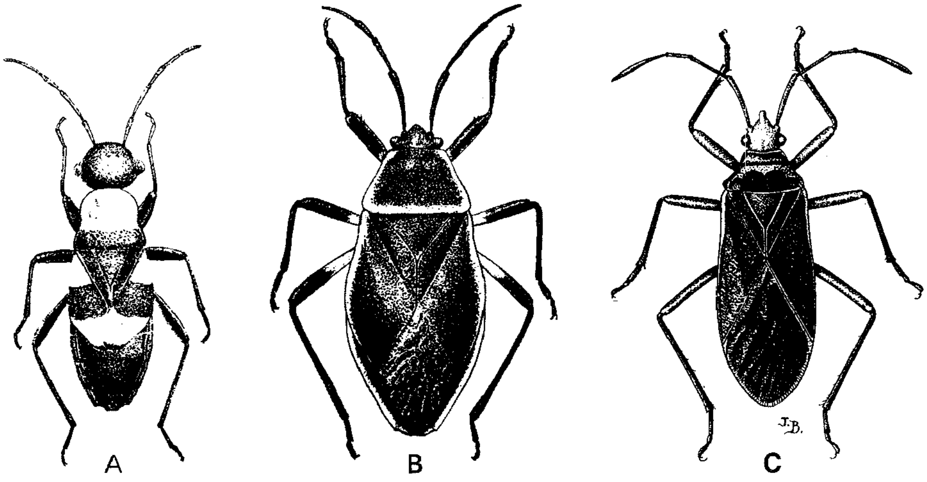


Figure 22–37 A, *Arhaphe carolina* (Herrick-Schäffer) (Largidae), 4×; B, *Largus succinctus* (L.) (Largidae), 3×; C, the cotton stainer, *Dysdercus suturellus* (Herrick-Schäffer) (Pyrrhocoridae), 4×. (A and B, courtesy of Froeschner and The American Midland Naturalist; C, courtesy of Slater and Baranowski and the Wm. C Brown Co.)

one (seven North American species), and its members are limited to the southern states.

Family **Coreidae—Leaf-Footed Bugs:** This is a moderate-sized group (about 80 North American species) whose members have well-developed scent glands. These glands open on the sides of the thorax between the middle and hind coxae (Figure 22–1B, sgo). Most species give off a distinct odor (sometimes pleasant, sometimes not) when handled. The coreids are mostly medium-sized to large, somewhat elongate, and dark-colored, with the head narrower and shorter than the pronotum (Figure 22–38A–C). Some species have the hind tibiae expanded and leaflike (Figure 22–38A), hence the name "leaf-footed bugs" for this group.

The Coreidae are plant feeders, but a few may be predaceous. The squash bug, *Anasa tristis* (DeGeer) (Figure 22–38C), a serious pest of cucurbits, is dark brown and about 13 mm long. It has one generation a year and passes the winter in the adult stage in debris and other sheltered places. The males of many species of coreids have the hind femora enlarged and armed with a series of sharp spines. These males establish territories and defend them vigorously from other males. The mesquite bug, *Thasus acutangulus* Stål, is one of the largest North American coreids (35–40 mm long). It is common on mesquite in Arizona and New Mexico. The nymphs form aggregations that, when disturbed, simultaneously produce a noxious vapor. If a tree with mesquite bugs on it is in a suburban yard, the homeowner may be considerably upset by the presence of so many big bugs.

Family **Alydidae—Broad-Headed Bugs:** These bugs are similar to the Coreidae, but the head is broad and nearly as long as the pronotum, and the body is usually long and narrow (Figure 22–38D). They might well be called "stink bugs," as they often "stink" much worse than the members of the Pentatomidae (to which the name "stink bug" is usually applied). They give off an odor reminiscent of someone with a bad case of halitosis. The openings of the scent glands are conspicuous oval openings between the middle and hind coxae. These bugs are fairly common on the foliage of weeds and shrubs along roadsides and in woodland areas. Most broad-headed bugs are either yellowish brown or black. Some of the black species have a red band across the middle of the dorsal side of the abdomen. A common brown species in the Northeast is *Protenor belfragei* Haglund; it is 12–15 mm long. Some of the black species (for example, *Alydus*; Figure 22–38D) look very much like ants in their nymphal stage, and the adults in the field look much like some of the spider wasps.

Family **Rhopalidae—Scentless Plant Bugs:** These bugs differ from the coreids in lacking well-developed scent glands. They are usually light-colored and smaller than the coreids (Figure 22–38E,F). Some are very similar to the orsilline lygaeids, but can be distinguished by the numerous veins in the membrane of the hemelytra (Figure 22–4D). They live principally on weeds, but a few (including the box elder bug) are arboreal. All are plant feeders.

The box elder bug, *Boisea trivittata* (Say), is a common and widely distributed species in this group. It is

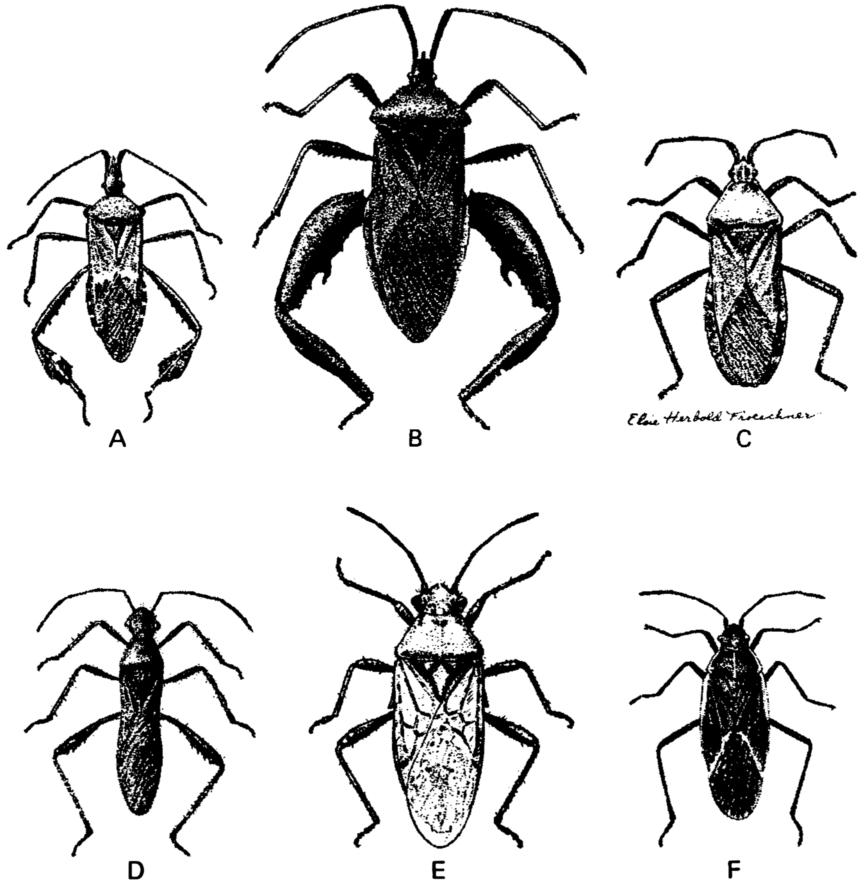


Figure 22–38 A, a leaf-footed bug, *Leptoglossus clypealis* (Heidemann), 1 ½×; B, *Acanthocephala femorata* (Fabricius), male (Coreidae), 1 ½×; C, the squash bug, *Anasa tristis* (DeGeer), 2×; D, a broad-headed bug, *Alydus eurinus* (Say), 2×; E, a scentless plant bug, *Arhyssus lateralis* (Say), 5×; F, the box elder bug, *Boisea trivittatus* (Say), 2×. (Redrawn from Froeschner.)

blackish with red markings and 11–14 mm long (Figure 22–38F). It often enters houses and other sheltered places in the fall, sometimes in considerable numbers. It feeds on box elder and occasionally other trees.

Family **Cydnidae—Burrower Bugs**: These bugs are a little like stink bugs in general appearance and antennal structure, but they are a little more oval and have the tibiae spiny (Figure 22–8A). They are black or reddish brown and less than 8 mm long (Figure 22–39B). They are usually found beneath stones or boards, in sand, or about the roots of grass tufts. They apparently feed on the roots of plants. The general collector is most likely to see them when they come to lights at night.

Family **Thyreocoridae**: These bugs are small (mostly 3–6 mm long), broadly oval, strongly convex, shining black bugs that are somewhat beetlelike in appearance (Figure 22–39A). The scutellum is very large and covers most of the abdomen and wings. These insects are common on grasses, weeds, berries, and flowers.

Family **Scutelleridae—Shield-Backed Bugs**: These look much like stink bugs (Pentatomidae), but the scutellum is very large and extends to the apex of the abdomen. The wings are visible only at the edge of the scutellum (Figure 22–40A). Most species in the northern part of the United States and Canada are brown or yellow, but many tropical species are brightly colored, even iridescent. The scutellerids are 8–10 mm long, and are plant feeders. Some species, particularly the sunn pest, *Eurygaster integriceps* Puton, are important pests of grain crops in Europe, central Asia, and the Middle East.

Family **Pentatomidae—Stink Bugs**: This is a large and well-known group (more than 200 North American species), and its members are easily recognized by their round or ovoid shape and 5-segmented antennae. They can be separated from other bugs having five-segmented antennae by the characters given in the key. Stink bugs are the most common and abundant of the bugs that produce a disagreeable odor, but some other bugs (particularly the broad-headed bugs) produce a more potent odor. Many stink bugs are brightly colored or conspicuously marked.

The family Pentatomidae is divided into five subfamilies, the Asopinae, Discocephalinae, Edessinae,

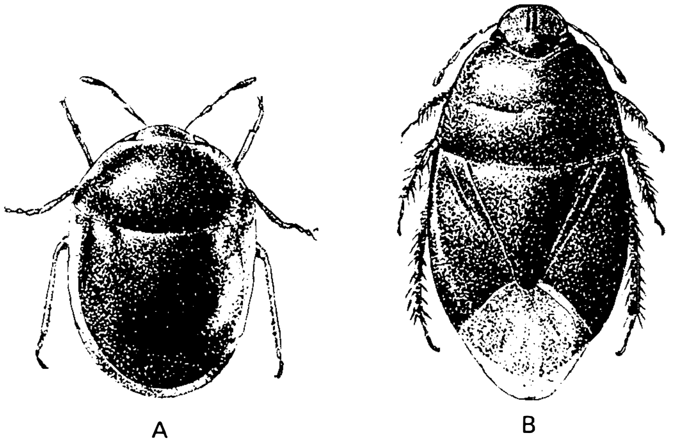


Figure 22–39 A, *Allocoris pulicaria* (Germar), 6½× (Thyreocoridae); B, a burrower bug, *Pangaeus bilineatus* (Say), 7½× (Cydnidae). (Courtesy of Froeschner and The American Midland Naturalist.)

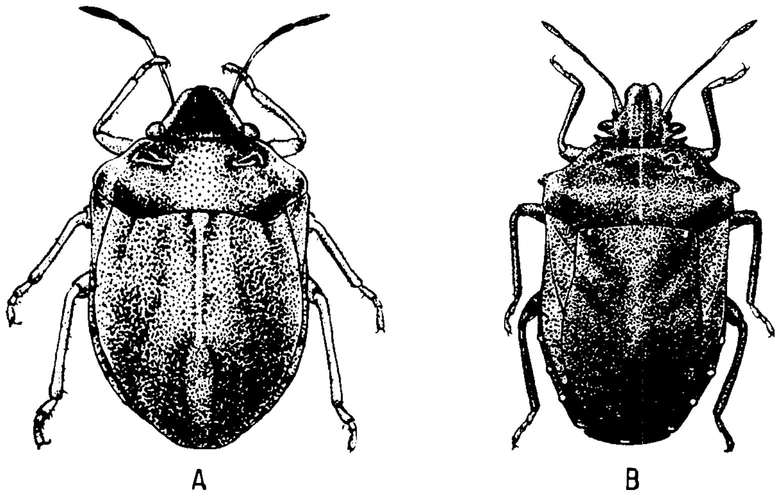


Figure 22–40 A, a shield-backed bug, *Homaemus parvulus* (Germar) (Scutelleridae); B, a terrestrial turtle bug, *Amaurochrous cinctipes* (Say), 8× (Pentatomidae). (Courtesy of Froeschner and The American Midland Naturalist.)

Podopinae, and Pentatominae. The last four, which contain most of the species in the family, are plant feeders, and the basal segment of the beak is slender and at rest lies between the bucculae, which are parallel. The Asopinae, which are predaceous, have a short, thick, basal segment of the beak, with only the base lying between the bucculae, which converge behind the beak.

The eggs of stink bugs, which are usually barrel-shaped and have the upper end ornamented with spines, are usually laid in groups, like many little brightly colored barrels lined up side by side (Figure 2–35).

One rather important pest species in this group is the harlequin bug (*Murgantia histrionica* (Hahn), Figure 22–41B). This brightly colored insect is often very destructive to cabbage and other cruciferous plants, particularly in the southern part of the United States. The southern green stink bug, *Nezara viridula* (L.), is an important pest of a wide variety of crops in the southeastern United States and throughout the world's tropics. The other stink bugs that are plant feeders (Figures 22–41A,C, 22–42) usually attack grasses or other plants and usually are not of very great economic importance. The spined soldier bug, *Podisus maculiventris* (Say) (Figure 22–41D), is predaceous on lepidopterous larvae. The terrestrial turtle bugs, *Amaurochrous* spp., 3.5–6.5 mm long, are similar to the shield-backed bugs, but may be separated by the characters given in the key (couplet 63). These were formerly placed in a family by themselves, the Podopidae, which has been reduced to the subfamily Podopinae.

Family **Acanthosomatidae:** This is a small group closely related to the Pentatomidae, but readily separated from them by having only two instead of three tarsal segments. The females of several of the species in North America guard the eggs and young nymphs.

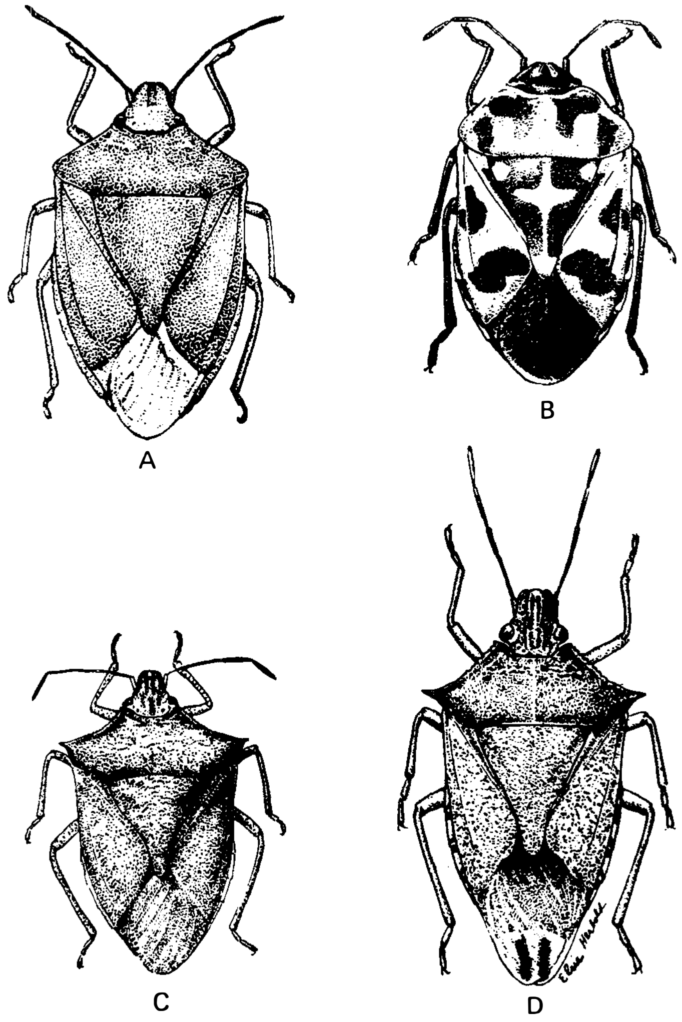


Figure 22–41 Stink bugs. A, *Thyanta custator* (Fabricius), 4½×; B, harlequin bug, *Murgantia histrionica* (Hahn), 4×; C, onespot stink bug, *Euschistus variolarius* (Palisot de Beauvois), 3×; D, spined soldier bug, *Podisus maculiventris* (Say), 4½×. A–C, Pentatominae; D, Asopinae. (Courtesy of Froeschner and The American Midland Naturalist.)

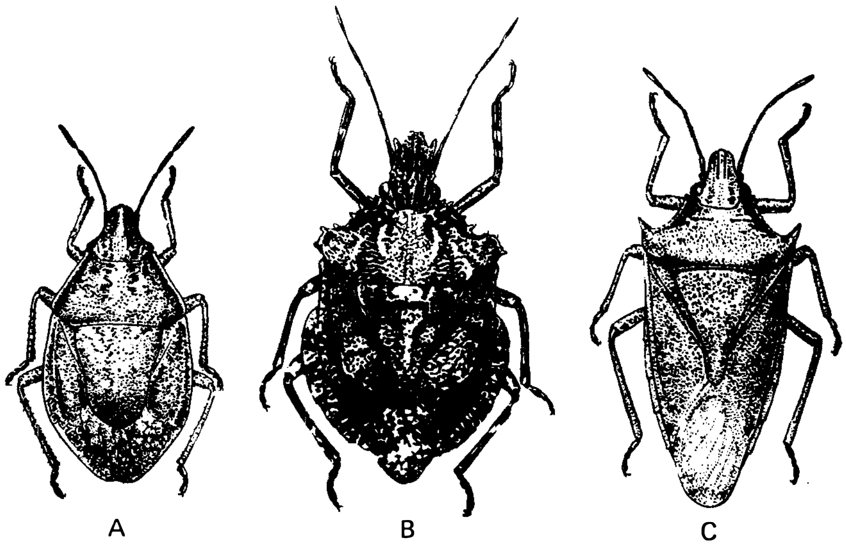


Figure 22–42 Stink bugs (subfamily Pentatominae). A, *Coenus delius* (Say), 3½×; B, *Brochymena arborea* (Say), 3×; C, *Oebalus pugnax* (Fabricius), 4½×. (Courtesy of Froeschner and the American Midland Naturalist.)

Elasmucha lateralis (Say) is fairly common on birch trees in the northern states and southern Canada.

SUBORDER Auchenorrhyncha: The members of the suborder Auchenorrhyncha (cicadas and hoppers) are active insects, being good fliers or jumpers. Their tarsi are three-segmented, and their antennae are very short and bristlelike. The cicadas are relatively large insects, with membranous wings and three ocelli. The hoppers are small to minute insects, with the front wings usually more or less thickened, and they usually have two ocelli (or none). The males of many Auchenorrhyncha can produce sound, but except for the cicadas these sounds are nearly inaudible to humans.

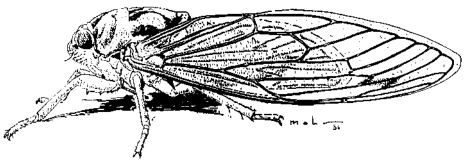
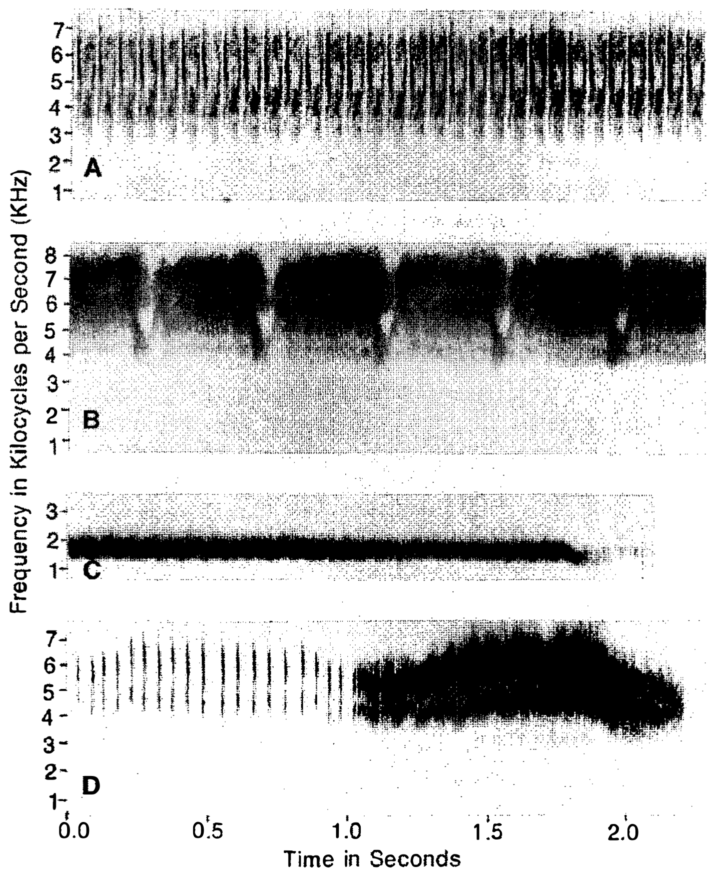


Figure 22–43 A dog-day cicada, *Tibicen pruinosa* (Say), about natural size. (Courtesy of Carl Mohr and the Illinois Natuaral History Survey.)

***Family* Cicadidae—Cicadas:** The members of this family can usually be recognized by their characteristic shape, their large size, and three ocelli (Figure 22–43). This group contains some of the largest Hemiptera in the United States, some of which reach a length of about 50 mm The smallest cicadas are a little less than 25 mm long. There are 157 species in 16 genera in the United States.

A conspicuous characteristic of cicadas is their ability to produce sound. Other Auchenorrhyncha (for example, leafhoppers) can make sounds, but their sounds are very weak and are detected through the substrate. The sounds produced by cicadas are generally quite loud. The sounds are made by the males, and each species has a characteristic song. Someone who is familiar with these songs can identify the species by song alone (Figure 22–44). Each species also produces a somewhat different sound (a disturbance squawk or "protest" sound) when handled or disturbed, and some species have a special song (termed a "courtship" song) that is produced by a male approaching a female.

Typical cicada sounds are produced by a pair of tymbals located dorsally at the sides of the basal abdominal segment in males (Figure 22–45, tmb). The



Donald J. Borror

Figure 22–44 Audiospectrographs of cicada calling songs. A, A dog-day cicada, *Tibicen chloromera* (Walker), about two seconds from near the middle of the song; B, another dog-day cicada, sometimes called the scissors-grinder cicada, *T. pruinosa* (Say), a portion of the song; C, a periodical cicada, *Magicicada septendecim* (L.), the end of the song; D, a part of the song of another periodical cicada, *M. cassini* (Fisher).

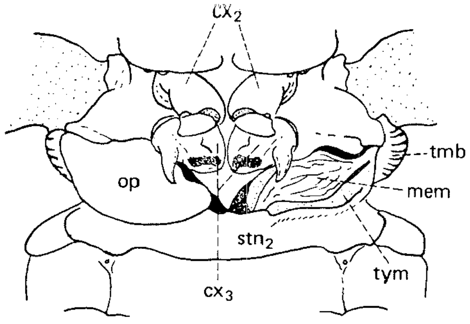


Figure 22–45 Thorax of a cicada (*Magicicada*), ventral view, showing the sound-producing organs; the operculum at the right has been removed. *cx*, coxa; *mem*, membrane; *op*, operculum; *stn*, abdominal sternum; *tmb*, tymbal; *tym*, tympanum.

tymbals consist of a posterior plate and several riblike bands lying in a membrane and are sometimes completely exposed above. In the dog-day cicadas (*Tibicen* spp.) they are covered above by an abdominal flap. The hearing organs, or tympana (*tym*), lie below the tymbals in a ventral cavity through which the tymbals or tymbal spaces are exposed below. This space often has a yellowish membrane (*mem*) connecting anteriorly to the thorax and is covered over ventrally by a pair of thoracic flaps called opercula (*op*). Internally, the last thoracic segment and up to five abdominal segments are nearly entirely filled by a large tracheal air sac that functions as a resonance chamber. A pair of large muscles runs through this air sac from above the tympana to the large plate of the tymbals, and their contractions cause the ribs to bend suddenly and produce the sounds. The air sacs and general body tension, plus other structures, control the volume and quality of the sounds. There are also stridulating and wing-banging groups of cicadas, which produce their characteristic sounds with their wings, sometimes in both sexes.

Two common types in this family are the dog-day cicadas (various species) (Figure 22–43) and the periodical cicadas (*Magicicada*). The dog-day cicadas are mostly large blackish insects, usually with greenish markings, that appear each year in July and August. The periodical cicadas, which occur in the eastern United States, differ from other eastern species in that they have reddish eyes and wing veins, they are smaller than most other eastern species, and the adults appear in late May and early June. The life cycle of dog-day cicadas is unknown, but two Japanese woodland species require 7 years to mature. The shortest known cicada life cycle is 4 years, for a grassland species. In dog-day cicadas, even with long life cycles, the generations overlap so that some adults appear each year. The life cycle of the periodical cicadas lasts 13 or 17 years, and in any given area adults are not present each year.

There are at twelve broods of 17-year cicadas and three of 13-year cicadas. These broods emerge as adults in different years and have different geographic ranges. The 17-year cicadas are generally northern and the 13-year cicadas southern, but there is considerable overlap, and both life-cycle types may occur in the same woods (but would emerge together only once every 221 years). The emergence of some of the larger broods is a very striking event, because the insects in these broods may be extremely numerous—up to 3.6 million per hectare.

There are seven species of periodical cicadas, three with a 17-year cycle and four with a 13-year cycle. The species in each life-cycle group differ in size, color, and song (see Table 22–1). Each 17-year species has a similar or sibling species with a 13-year cycle, from which it can be separated only by differences in life cycle and distribution. Most broods of each life-cycle type contain more than one species, and many contain all three.

Most cicadas insert their eggs in living or dead twigs of trees and shrubs, some in grasses and forbs. Living twigs are usually so severely injured by this egg laying that the terminal part of the twig dies. The eggs generally hatch in a month or so (some species overwinter as eggs), and the nymphs drop to the ground, enter the soil, and feed on roots, particularly of perennial plants. The nymphs remain in the ground until they are ready to molt the last (fifth) time. In the case of the periodical cicadas, this period is 13 to 17 years. When the last nymphal instar digs its way out of the ground, it climbs up on some object, usually a tree, and fastens its claws in the bark, and the final molt then takes place. The adult stage lasts a month or more.

The principal damage done by cicadas is caused by the egg laying of the adults. When the adults are numerous, as in years when the periodical cicadas emerge, they may do considerable damage to young trees and nursery stock.

Family **Membracidae—Treehoppers:** Most members of this group can be recognized by the large pronotum that covers the head, extends back over the abdomen, and often assumes peculiar shapes (Figure 22–46). Many species appear more or less humpbacked. Others have spines, horns, or keels on the pronotum, and some species are shaped like thorns. The wings are largely concealed by the pronotum. These insects are rarely more than 10 or 12 mm long.

Treehoppers feed chiefly on trees and shrubs, and most species feed only on specific types of host plants. Some species feed on grass and herbaceous plants in

Table 22–1 Summary of the Periodical Cicadas (*Magicicada*)[a]

Characteristics	17-Year Cycle	13-Year Cycle
Body length 27–33 mm Propleura and lateral extensions of pronotum between eyes and wing bases reddish Abdominal sterna primarily reddish brown or yellow Song: "phaaaaaroah," a low buzz, 1–3 seconds in length, with a drop in pitch at the end (Figure 22–44C)	Linnaeus' 17-year cicada, *M. septendecim* (L.)	Riley's 13-year cicada, *M. tredecim* Walsh and Riley
Body length 20–28 mm Propleura and lateral extensions of pronotum between eyes and wing bases black Abdominal sterna all black, or a few with a narrow band of reddish brown or yellow on apical third; this band often constricted or interrupted medially Last tarsal segement with apical half or more black Song: 2–3 seconds of ticks alternating with 1- to 3-second buzzes that rise and then fall in pitch and intensity (Figure 22–44D)	Cassin's 17-year cicada, *M. cassini* (Fisher)	Cassin's 13-year cicada, *M. tredecassini* Alexander and Moore
Body length 19–27 mm Propleura and lateral extensions of pronotum between eyes and wing bases black Abdominal sterna black basally, with a broad apical band of reddish yellow or brown on posterior half of each sternum; this band not interrupted medially Last tarsal segment entirely brownish or yellowish or, at most, the apical third black Song: 20–40 short high-pitched phrases, each like a short buzz and tick delivered together, at the rate of 3–5 per second, the phrases shorter and lacking the short buzz	The little 17-year cicada, *M. septendecula* Alexander and Moore	The little 13-year cicada, *M. tredecula* Alexander and Moore

[a] Data from Alexander and Moore (1962).

the nymphal stage. The treehoppers have one or two generations a year and usually pass the winter in the egg stage.

Only a few species in this group are considered of economic importance, and most of their damage is caused by egg laying. The buffalo treehopper, *Stictocephala bizonia* Kopp and Yonke (Figure 22–46C), is a common pest species that lays its eggs in the twigs of apple and several other trees. The eggs are placed in slits cut in the bark, and the terminal portion of the twig beyond the eggs often dies. The eggs overwinter and hatch in the spring, and the nymphs drop to herbaceous vegetation where they complete their development, returning to the trees to lay their eggs.

***Family* Aetalionidae:** Two genera in this family occur in North America: *Microcentrus*, which is widely distributed, and *Aetalion*, which occurs in Florida, southern Arizona, and California. *Microcentrus* resembles a membracid, but the pronotum has only a narrow median backward-projecting process that extends a short distance between the wings and only partly covers the scutellum (Figure 22–13A). It was formerly placed in the subfamily Centrotinae of the Membracidae, but Hamilton (1971) transferred it to the family Aetalionidae. *Aetalion* resembles a large cercopid, but lacks spines on the hind tibiae characteristic of that group. The pronotum extends farther forward over the head (Figure 22–13B), and the face is vertical. The beak in the aetalionids extends to the hind coxae. The beak is shorter in most other hoppers, but is even longer in some cercopids (extending beyond the hind coxae in *Aphrophora* of the Cercopidae). *Microcentrus caryae* (Fitch), a widely distributed species, lives on hickory, oak, and other trees. *Aetalion* also lives on trees and is sometimes tended by ants or (in the tropics) meliponine bees (Apidae).

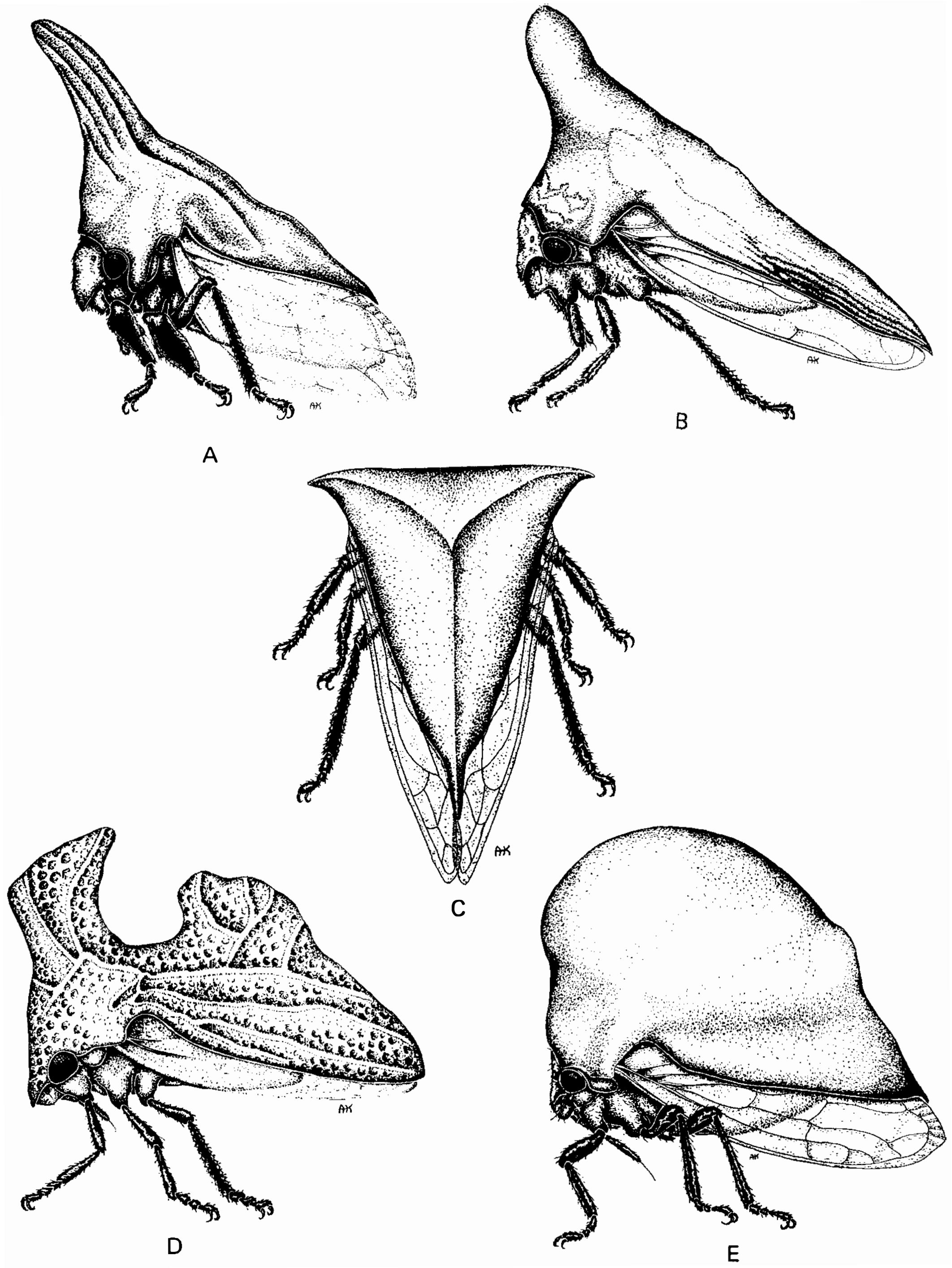


Figure 22–46 Treehoppers. A, *Campylenchia latipes* (Say); B, *Thelia bimaculata* (Fabricius); C, *Stictocephala bizonia* (Kopp and Yonke); D, *Entylia concisa* Walker; E, *Archasia galeata* (Fabricius). A, B, D, and E, lateral views; C, dorsal view.

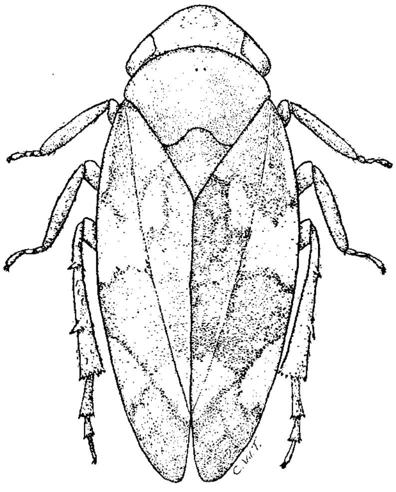


Figure 22–47 A froghopper, *Philaenus spumarius* (L.).

Family **Cercopidae—Froghoppers or Spittlebugs:** Froghoppers are small, hopping insects, rarely over 13 mm long, some species of which vaguely resemble tiny frogs in shape (Figure 22–47). They are very similar to the leafhoppers, but can be distinguished by the spination of the hind tibiae (Figure 22–14A,B). They are usually brown or gray. Some species have a characteristic color pattern.

These insects feed on shrubs, trees, and herbaceous plants, the different species feeding on different host plants. The nymphs surround themselves with a frothy mass (Figure 22–48) and are usually called "spittlebugs." These masses of foam are sometimes quite abundant in meadows. Each mass contains one or more greenish or brownish spittlebugs. After the last molt the insect leaves the foam and moves about actively.

The foam is made from fluid voided from the anus and from a mucilaginous substance secreted by the epidermal glands on the seventh and eighth abdominal segments. Air bubbles are introduced into the foam by means of the caudal appendages of the insect. A spittlebug usually rests head downward on the plant, and as the foam forms, it flows down over and covers the insect. It lasts some time, even when exposed to heavy rains, and provides the nymph with a moist habitat. The adults do not produce foam.

The most important economic species of spittlebug in the eastern states is *Philaenus spumarius* (L.) (Figure 22–47), a meadow species that causes serious stunting, particularly to clovers. This insect lays its eggs in late summer in the stems or sheaths of grasses and other plants, and the eggs hatch the following spring. There is one generation a year. There are several color forms of this species. Most of the spittlebugs at-

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Figure 22–48 Foam mass of the spittlebug *Philaenus spumarius* (L.).

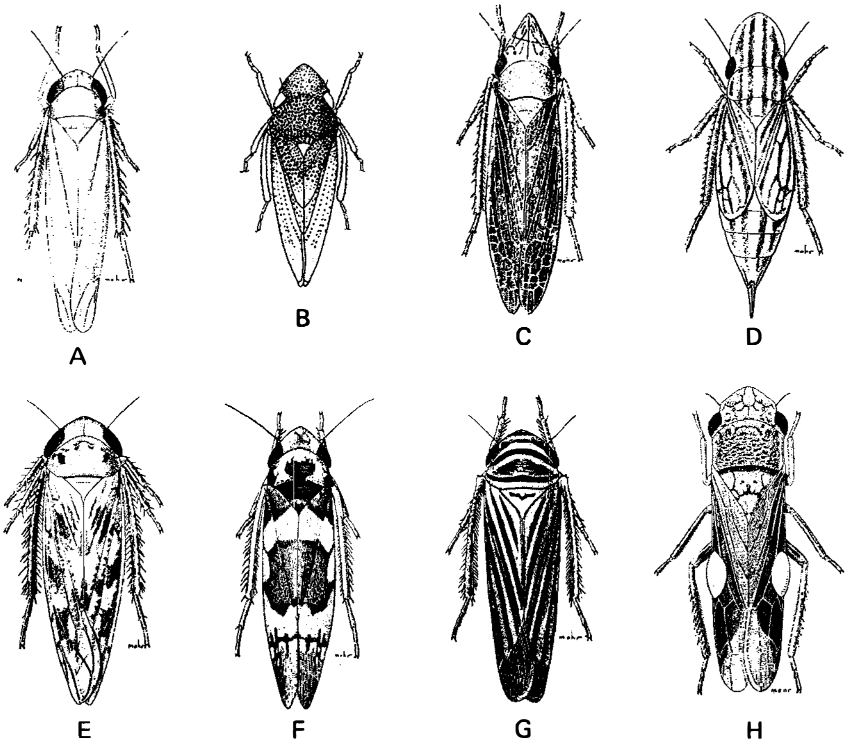

Figure 22–49 Leafhoppers. A, the potato leafhopper, *Empoasca fabae* (Harris) (Typhlocybinae); B, *Xerophloea major* Baker (Ledrinae); C, *Draeculacephala mollipes* (Say) (Cicadellinae); D, *Hecalus lineatus* (Uhler) (Hecalinae); E, the beet leafhopper, *Circulifer tenellus* Baker (Deltocephalinae); F, *Erythroneura vitis* (Harris) (Typhlocybinae); G, *Tylozygus bifidus* (Say) (Cicadellinae); H, *Oncometopia undata* (Fabricius) (Cicadellinae). (Courtesy of the Illinois Natural History Society.)

tack grasses and herbaceous plants, but a few attack trees; *Aphrophora permutata* Uhler and *A. saratogensis* (Fitch) are important pests of pine.

***Family* Cicadellidae—Leafhoppers**: The leafhoppers constitute a very large group (about 2500 North American species), and they are of various forms, colors, and sizes (Figure 22–49). They are similar to froghoppers and aetalionids in the genus *Aetalion*, but they have one or more rows of small spines extending the length of the hind tibiae. They rarely exceed 13 mm long, and many are only a few millimeters long. Many are marked with a beautiful color pattern.

Leafhoppers live on almost all types of plants, including forest, shade, and orchard trees, shrubs, grasses, and many field and garden crops. They feed principally on the leaves of their food plant. The food of most species is quite specific, and the habitat is therefore well defined. In many cases a specialist in this group can examine a series of specimens taken in a given habitat and can describe that habitat and often determine the general region of the country from which the specimens came.

Most leafhoppers have a single generation a year, but a few have two or three. The winter is usually passed in either the adult or the egg stage, depending on the species.

There are many economically important pest species in this group, and they cause five major types of injury to plants. (1) Some species remove excessive amounts of sap and reduce or destroy the chlorophyll in the leaves, causing the leaves to become covered with minute white or yellow spots. With continued feeding, the leaves turn yellowish or brownish. This type of injury is produced on apple leaves by various species of *Erythroneura*, *Typhlocyba*, and *Empoasca*. (2) Some species interfere with the normal physiology of the plant, for example, by mechanically plugging the phloem and xylem vessels in the leaves so that transport of food materials is impaired. A browning of the outer portion of the leaf, and eventually of the entire leaf, results. The potato leafhopper, *Empoasca fabae* (Harris) (Figure 22–49A), causes this type of injury. (3) A few species injure plants by ovipositing in green twigs, often causing the terminal portion of the twigs to die. Various species of *Gyponana* cause damage of this sort. Their egg punctures are similar to those of the buffalo treehopper but smaller. (4) Many species of leafhoppers act as vectors of the organisms that cause plant diseases. Aster yellows, corn stunt, phloem necrosis of elm, Pierce's disease of grape, phony peach, potato yellow dwarf, curly top in sugar beets, and other plant diseases are transmitted by leafhoppers, chiefly species in the subfamilies Agalliinae, Cicadellinae, and Deltocephalinae. (5) Some species cause stunting and leaf curling that result from the inhibition of growth on the undersurface of the leaves where the leafhoppers feed. The potato leafhopper, *Empoasca fabae*, also produces injury of this type.

Many species of leafhoppers emit from the anus a liquid called "honeydew." It consists of unused portions of plant sap to which are added certain waste products of the insect.

Many of the leafhoppers (as well as some of the other hoppers) produce sound (Ossiannilsson, 1949). These sounds are all quite weak; some can be heard if the insect is held close to one's ear, whereas others can only be heard when amplified. These sounds are produced by the vibration of tymbals located dorsolaterally at the base of the abdomen (on the first or second segment). The tymbals are thin-walled areas of the body wall, and are not very conspicuous from an external view. The sounds produced by leafhoppers of the genus *Empoasca* (Shaw et al. 1974) are of up to five types (depending on the species): one or two types of "common" sounds, disturbance sounds, courtship sounds, and sounds by the female. Most of these sounds are different in different species and are believed to play a role in species recognition by the insects.

Some authorities have considered the leafhoppers to represent a superfamily (the Cicadelloidea) and divided them into a number of families. The differences between these families are not as great as those between the families of Fulgoroidea, and most leafhopper specialists prefer to treat the leafhoppers as a single family divided into subfamilies. There are differences of opinion as to the leafhopper subfamilies to recognize and the names to give them. The arrangement we follow in this book is outlined here, with other names and arrangements in parentheses. Following each subfamily is a list of the genera in that group mentioned in this book.

Family Cicadellidae
  Ledrinae (Xerophloeinae)—*Xerophloea*
  Dorycephalinae (Dorydiinae in part)—*Dorycephalus*
  Megophthalminae (Ulopinae; Agalliinae in part)
  Agalliinae—*Aceratagallia, Agallia, Agalliana, Agalliopsis*
  Macropsinae—*Macropsis*
  Idiocerinae (Eurymelinae)—*Idiocerus*
  Gyponinae—*Gyponana*
  Iassinae (including Bythoscopinae)
  Penthimiinae—*Penthimia*
  Koebeliinae—*Koebelia*
  Coelidiinae (Jassinae)—*Tinobregmus*
  Nioniinae—*Nionia*
  Aphrodinae—*Aphrodes*
  Xestocephalinae—*Xestocephalus*
  Neocoelidiinae—*Paracoelidia*
  Cicadellinae (Tettigellinae, Tettigoniellinae; including Evacanthinae)—*Agrosoma, Carneocephala, Cuerna, Draeculacephala, Friscanus, Graphocephala, Helochara, Homalodisca, Hordnia, Keonolla, Neokolla, Oncometopia, Pagaronia, Sibovia, Tylozygus*
  Typhlocybinae (Cicadellinae)—*Empoasca, Erythroneura, Kunzeana, Typhlocyba*
  Deltocephalinae (Athysaninae, Hecalinae Euscelinae; including Balcluthinae)—*Acinopterus, Chlorotettix, Circulifer, Colladonus, Dalbulus, Endria, Euscelidius, Euscelis, Excultanus, Fieberiella, Graminella, Hecalus Macrosteles, Norvellina, Paraphlepsius, Paratanus, Pseudotettix, Scaphoideus, Scaphytopius, Scleroracus, Texananus*

Key to the Subfamilies of Cicadellidae

1.	Front wings without crossveins basad of apical crossveins (Figure 22–50F); longitudinal veins indistinct basally; ocelli often absent; apex of first segment of hind tarsus sharp-tipped; slender, fragile leafhoppers	Typhlocybinae	p. 315
1′.	Front wings with crossveins basad of apical crossveins (Figure 22–50H); longitudinal veins distinct basally; ocelli present; apex of first segment of hind tarsus truncate; usually relatively robust leafhoppers	2	
2(1′).	Episterna of prothorax easily visible in anterior view, not largely concealed by genae (Figure 22–50A, eps$_1$)	3	
2′.	Episterna of prothorax largely or entirely concealed by genae in anterior view (Figure 22–50B–E,G)	4	

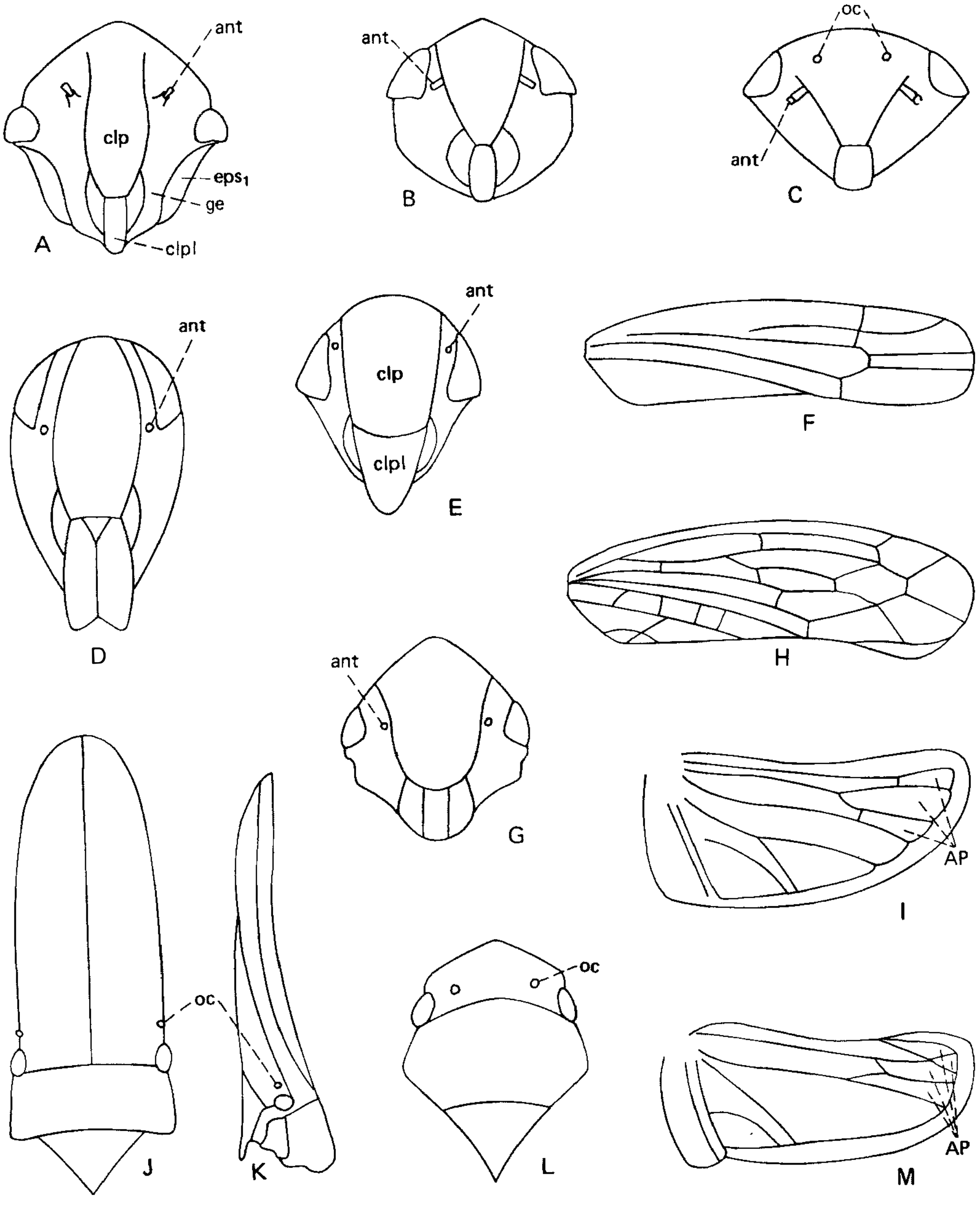

Figure 22–50 Characters of leafhoppers. A, face of *Xerophloea viridis* (Fabricius) (Ledrinae); B, face of *Paraphlepsius irroratus* (Say) (Deltocephalinae); C, face of *Idiocerus alternatus* (Fitch) (Idiocerinae); D, face of *Tinobregmus vittatus* Van Duzee (Coelidiinae); E, face of *Sibovia occatoria* (Say) (Cicadellinae); F, front wing of *Kunzeana marginella* (Baker) (Typhlocybinae); G, face of *Parabolocratus viridis* (Uhler) (Hecalinae); H, front wing of *Endria inimica* (Say) (Deltocephalinae); I, hind wing of *Macropsis viridis* (Fitch) (Macropsinae); J, head, pronotum, and scutellum of *Dorycephlus platyrhynchus* (Osborn), dorsal view (Dorycephalinae); K, same, lateral view; L, head, pronotum, and scutellum of *Xerophloea viridis* (Fabricius), dorsal view (Ledrinae); M, hind wing of *Aceratagallia sanguinolenta* (Provancher) (Agalliinae). *ant*, antennae; *AP*, apical cells; *clp*, clypeus; *clpl*, clypellus; *eps*$_1$, episternum of prothorax; *ge*, gena; *oc*, ocellus.

3(2).	Ocelli on crown, remote from eyes and from anterior margin of crown (Figure 22–50L); dorsum covered with rounded pits (Figure 22–49B)	Ledrinae	p. 314
3′.	Ocelli on lateral margins of head, just in front of eyes (Figure 22–50J,K); dorsum not covered with rounded pits	Dorycephalinae	p. 314
4(2′).	Ocelli on crown (usually disk of crown), frontal sutures extending over margin of crown nearly to ocelli; clypellus broad above and narrowed below; clypeus usually swollen (Figure 22–50E)	Cicadellinae	p. 315
4′.	Without combination of characters in preceding entry	5	
5(4′).	Frontal sutures terminating at or slightly above antennal pits, or ocelli near disk of crown and remote from eyes, or both	6	
5′.	Frontal sutures extending beyond antennal pits to or near ocelli, ocelli never on disk of crown	11	
6(5).	Lateral margins of pronotum carinate, moderately long; ledge or carina above antennal pits transverse or nearly so	7	
6′.	Lateral margins of pronotum short and not carinate, or only feebly so; ledge above antennal pits, if present, oblique	9	
7(6).	Face in profile concave; front wings with appendix very large, first (inner) apical cell large (equal in area to second and third apical cells combined)	Penthimiinae	p. 314
7′.	Face in profile not concave, usually distinctly convex; front wings with appendix normal or small, first apical cell not enlarged	8	
8(7′).	Ocelli on crown, usually remote from anterior margin of head	Gyponinae	p. 314
8′.	Ocelli on anterior margin of crown	Iassinae	p. 314
9(6′).	Hind wings always present, with 3 apical cells (Figure 22–50I, AP); pronotum extending forward beyond anterior margins of eyes; distance between ocelli usually greater than twice the distance from ocellus to eye	Macropsinae	p. 314
9′.	Hind wings present or absent, if present with 4 apical cells (Figure 22–50M, AP); pronotum not extending forward beyond anterior margins of eyes; distance between ocelli not more than twice distance from ocellus to eye	10	
10(9′).	Face with carinae replacing frontal sutures above antennal pits; western United States	Megophthalminae	p. 314
10′.	Face without such carinae; widely distributed	Agalliinae	p. 314
11(5′).	Dorsum with circular pits; pronotum extending forward beyond anterior margins of eyes; shining black leafhoppers	Nioniinae	p. 315
11′.	Dorsum without such pits; pronotum not extending forward beyond anterior margins of eyes; color variable	12	
12(11′).	Distance between ocelli less than distance between antennal pits, or clypellus much wider distally than basally and extending to or beyond apex of genae	13	
12′.	Distance between ocelli equal to or greater than distance between antennal pits, or clypellus parallel-sided and usually not extending to apex of genae	14	
13(12).	Clypeus long and narrow, of nearly uniform width (Figure 22–50D); crown not wider than eye; costal margin of hind wings of macropterous forms expanded for short distance near base; head narrower than pronotum	Coelidiinae	p. 315
13′.	Clypeus short, broad, wider above (Figure 22–50C); crown wider than eye; costal margin of hind wings not expanded basally; head usually wider than pronotum	Idiocerinae	p. 314

14(12′).	Ocelli on face	Koebeliinae	p. 314
14′.	Ocelli on or near margin of head	15	
15(14′).	Clypeus extended laterally over bases of antennae, thus forming relatively deep antennal pits; small leafhoppers with head rounded, eyes small, clypeus ovate, antennae near margin of eyes, and ocelli distant from eyes	Xestocephalinae	p. 315
15′.	Clypeus not extended laterally over bases of antennae to form antennal pits; variable leafhoppers, but not having combination of characters in preceding entry	16	
16(15′).	Distinct ledge or carina above each antennal pit	17	
16′.	Without ledge or carina above each antennal pit	Deltocephalinae	p. 315
17(16).	Ledge above each antennal pit oblique; face strongly convex (viewed from above)	Neocoelidiinae	p. 315
17′.	Ledge above each antennal pit transverse; face broad and relatively flat	Aphrodinae	p. 315

Subfamily **Ledrinae:** This group is represented in North America by about eight species of *Xerophloea*. They are grass feeders and sometimes become pests of forage crops. They have the dorsum covered with numerous pits, and the ocelli are on the disk of the crown (Figure 22–49B).

Subfamily **Dorycephalinae:** This is another small group (about nine North American species) of grass feeders, and they are chiefly southern in distribution. They are elongate and somewhat flattened. The head is long, with the margin thin and foliaceous (Figure 22–50J,K).

Subfamily **Megophthalminae:** The members of this small group (seven North American species) are known only from California. Their food plants are unknown.

Subfamily **Agalliinae:** This is a fairly large group (about 70 North American species) in which the head is short, the ocelli are on the face, and the frontal sutures terminate at the antennal pits. The food habits of these leafhoppers are rather varied. A few species in this group act as vectors of plant diseases. For example, species of *Aceratagallia*, *Agallia*, and *Agalliopsis* serve as vectors of potato yellow dwarf.

Subfamily **Macropsinae:** In this group (more than 50 North American species) the head is short and broad, and the ocelli are on the face. The anterior margin of the pronotum extends forward beyond the anterior margins of the eyes. The dorsal surface, from the crown to the scutellum, is somewhat roughened—rugulose, punctate, or striate. These leafhoppers feed on trees and shrubs.

Subfamily **Idiocerinae:** This group (about 75 North American species) is similar to the Macropsinae, but the pronotum does not extend forward beyond the anterior margins of the eyes. These leafhoppers also feed on trees and shrubs.

Subfamily **Gyponinae:** This is a large group (more than 140 North American species) of relatively robust and somewhat flattened leafhoppers, which have their ocelli on the crown remote from their eyes and back from the anterior margin of the head. The crown is variable in shape and may be produced and foliaceous or short and broadly rounded in front. Some species feed on herbaceous plants, and others feed on trees and shrubs. One species, *Gyponana angulata* (Spangberg), acts as a vector of aster yellows, and another, *G. lamina* DeLong, acts as a vector of peach X-disease.

Subfamily **Iassinae:** These leafhoppers are relatively robust and somewhat flattened, with a short head and the ocelli on the anterior margin of the crown, about midway between the eyes and the apex of the head. The group is small (23 North American species), and its members live chiefly in the West. Little is known about their food plants; but some species are known to feed on shrubs.

Subfamily **Penthimiinae:** This group is represented in North America by only two species of *Penthimia*, which occur in the East. They are short, oval, and somewhat flattened. The ocelli are located on the crown about halfway between the eyes and the midline, and the front wings are broad with a large appendix. Their food plants are not known.

Subfamily **Koebeliinae:** This group is represented in the United States by four species of *Koebelia*, which occur in the West and feed on pine. The head is wider than the pronotum, and the crown is flat with a foliaceous margin and a broad, shallow furrow in the midline. The ocelli are on the face.

Subfamily Coelidiinae: This is a small group (10 North American species) of relatively large and robust leafhoppers. The clypeus is long and narrow and of nearly uniform width (Figure 22–50D; in most other leafhoppers, the clypeus is wider dorsally). The head is narrower than the pronotum, with the eyes large and the crown small, and the ocelli are on the anterior margin of the crown. This group is mainly Neotropical, and its known food plants are shrubs and herbaceous plants.

Subfamily Nioniinae: This group is represented in North America by a single species, *Nionia palmeri* (Van Duzee), which occurs in the southern states. Its food plants are not known. This leafhopper is shining black, with the crown short and broad, and with the ocelli on the anterior margin and distant from the eyes. The anterior margin of the pronotum extends forward beyond the anterior margins of the eyes, and the anterior part of the dorsum bears numerous circular pits.

Subfamily Aphrodinae: This is a small group (six North American species), but its members are common and widely distributed. They are short, broad, and somewhat flattened, with the ocelli on the anterior margin of the crown. The head and pronotum are rugulose or coarsely granulate. Species of *Aphrodes* are known to act as vectors of aster yellows, clover stunt, and clover phyllody.

Subfamily Xestocephalinae: This is a small group (three species of *Xestocephalus*) but a widely distributed one, whose members are small and robust, with the head and eyes small. The crown is rounded anteriorly, with the ocelli on the anterior margin.

Subfamily Neocoelidiinae: This is a small group (26 North American species), and many of its members are rather elongate in form. The face is strongly convex, and the ocelli are on the crown near the anterior margin and the eyes. Some species (*Paracoelidia*) live on pine.

Subfamily Cicadellinae: This is a fairly large group (nearly a hundred North American species), with many common species. Most species are relatively large, and some are rather robust. The ocelli are on the crown, and the frontal sutures extend over the margin of the head nearly to the ocelli. Some members of this group are very strikingly colored. One of our largest and most common species is *Graphocephala coccinea* (Foerster), which is similar in size and shape to *Draeculacephala mollipes* (Say) (Figure 22–49C), but has the wings reddish striped with bright green. The nymphs of this species are bright yellow. This species is often found on forsythia and other ornamental shrubs. Many species in this group serve as vectors of plant disease: species of *Carneocephala, Cuerna, Draeculacephala, Friscanus, Graphocephala, Helochara, Homalodisca, Neokolla, Oncometopia,* and *Pagaronia* serve as vectors of Pierce's disease of grape; and species of *Draeculacephala, Graphocephala, Homalodisca,* and *Oncometopia* serve as vectors of phony peach.

Subfamily Typhlocybinae: This is a large group (more than 700 North American species, more than half of which are in the genus *Erythroneura*) of small, fragile, and often brightly colored leafhoppers (Figure 22–49A,F). The ocelli may be present or absent, and the venation of the front wings is somewhat reduced, with no crossveins except in the apical portion. The food plants are varied. This group includes a number of pest species in the genera *Empoasca, Erythroneura,* and *Typhlocyba.*

Subfamily Deltocephalinae: This is the largest subfamily of leafhoppers (more than 1150 North American species), and its members vary in form and food plants. The ocelli are always on the anterior margin of the crown, and there is no ledge above the antennal pits. Many members of this group are important vectors of plant diseases. Aster yellows is transmitted by species of *Scaphytopius, Macrosteles, Paraphlepsius,* and *Texananus*. Curly top of sugar beets is transmitted by *Circulifer tenellus* (Baker). Phloem necrosis of elm is transmitted by *Scaphoideus luteolus* Van Duzee. Clover phyllody is transmitted by species of *Macrosteles, Chlorotettix, Colladonus,* and *Euscelis.* Corn stunt is transmitted by species of *Dalbulus* and *Graminella.*

SUPERFAMILY Fulgoroidea—Planthoppers: This is a large group, but its members are seldom as abundant as the leafhoppers or froghoppers. The species in the United States are usually no more than 10 or 12 mm long, but some tropical species reach a length of 50 mm or more. Many of the planthoppers have the head peculiarly modified, with that part in front of the eyes greatly enlarged and more or less snoutlike (Figure 22–51, especially G–I).

The planthoppers differ from the leafhoppers in having only a few large spines on the hind tibiae and from both the leafhoppers and the froghoppers in having the antennae arising below the compound eyes. The ocelli are usually located immediately in front of the eyes, on the side (rather than the front or dorsal surface) of the head (Figure 22–9C). There is often a sharp angle separating the side of the head (where the compound eyes, antennae, and ocelli are located) and the front.

The food plants of these insects range from trees and shrubs to herbaceous plants and grasses. The planthoppers feed on the plant juices and, like many other Auchenorrhyncha and Sternorrhyncha, produce honeydew. Many of the nymphal forms are ornamented with wax filaments. Very few planthoppers cause economic damage to cultivated plants.

***Family* Delphacidae:** This is the largest family of planthoppers, and its members can be recognized by

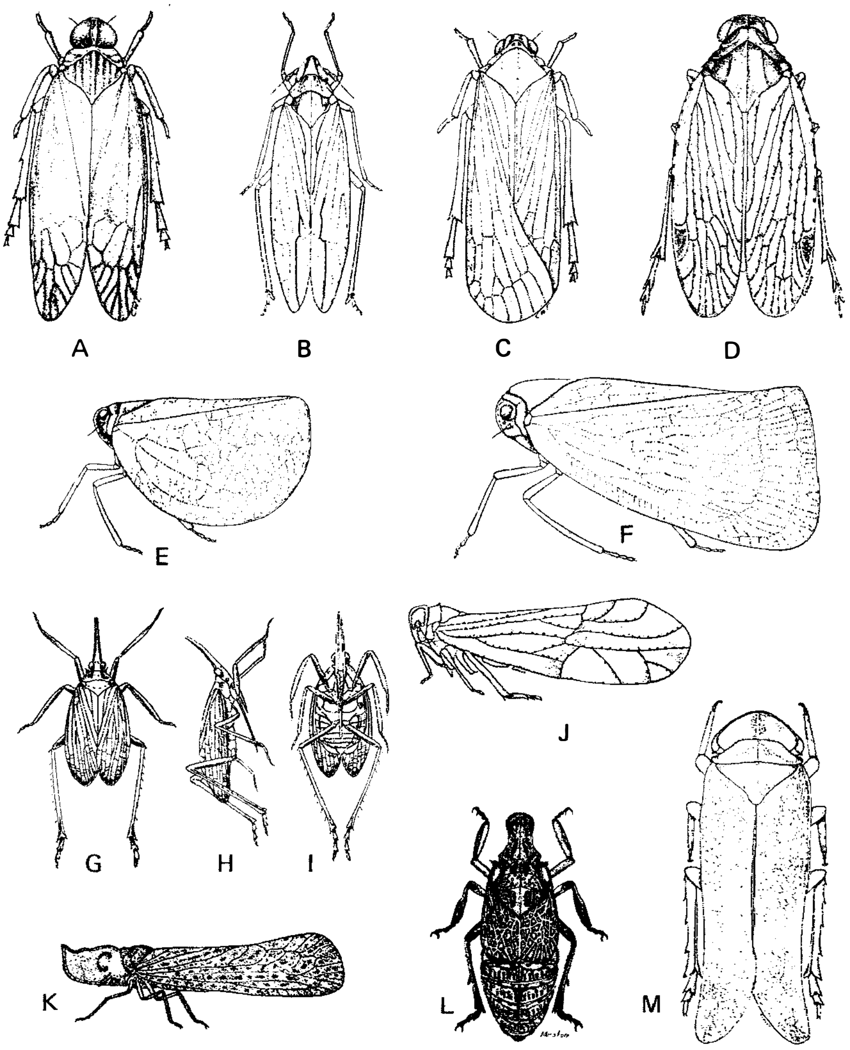

Figure 22–51 Planthoppers. A, *Oecleus borealis* Van Duzee (Cixiidae); B, *Sternocranus dorsalis* Fitch (Delphacidae); C, *Catonia impunctata* (Fitch) (Achilidae); D, *Cixius angustatus* Caldwell (Cixiidae); E, *Acanalonia bivittata* (Say) (Acanaloniidae); F, *Anormenis septentrionalis* (Spinola) (Flatidae); G, **H**, and I, *Scolops perdix* Uhler (Dictyopharidae), dorsal, lateral, and ventral views; J, *Liburniella ornata* (Stål) (Delphacidae); K, *Apache degeerii* (Kirby) (Derbidae); L, *Fitchiella robertsoni* (Fitch) (Issidae); M, *Cyrpoptus belfragei* Stål (Fulgoridae). (Courtesy of Osborn and the Ohio Biological Survey.)

the large, flattened spur at the apex of the hind tibiae (Figure 22–10C, sp). Most species are small, and many have reduced wings. The sugarcane leafhopper, *Perkinsiella saccharicida* Kirkaldy, which at one time was a very destructive pest in Hawaii, is a member of this family.

***Family* Derbidae:** These planthoppers are principally tropical and feed on woody fungi. Most species are elongate with long wings and are rather delicate in build (Figure 22–51K).

***Family* Cixiidae:** This is one of the larger families of planthoppers. Its members are widely distributed, but most species are tropical. Some species are subterranean feeders on the roots of grasses during their nymphal stage. The wings are hyaline and frequently ornamented with spots along the veins (Figure 22–51A,D).

Family **Kinnaridae:** These planthoppers resemble the Cixiidae, but are quite small and have no dark spots on the wings. Our six species (*Oeclidius*) occur in the Southwest, but some West Indies species may occur in southern Florida.

Family **Dictyopharidae:** The members of this group are chiefly grass feeders and are generally found in meadows. The most common eastern members of this group (*Scolops*, Figure 22–51G–I) have the head prolonged anteriorly into a long, slender process. Other dictyopharids have the anterior portion of the head somewhat triangularly produced or not at all produced.

Family **Fulgoridae:** This group contains some of the largest planthoppers, some tropical species having a wingspread of about 150 mm. The largest North American fulgorids have a wingspread of a little more than 25 mm and a body length of about 13 mm. Some tropical species have the head greatly inflated anteriorly, producing a peanutlike process. Early entomologists, having never seen living specimens, believed this to be luminous, thereby giving rise to the name "lanternflies" for these insects. Most North American species (for example, Figure 22–51M) have a short head. The members of this family can generally be recognized by the reticulated anal area of the hind wings.

Family **Achilidae:** These planthoppers can usually be recognized by their overlapping front wings (Figure 22–51C). Most species are brownish, and vary in length from about 4 to 10 mm. The nymphs usually live under loose bark or in a depression in dead wood.

Family **Tropiduchidae:** This is a tropical group, but three species have been found in Florida and the family extends as far west as Louisiana. The most common is probably *Pelitropis rotulata* Van Duzee, which has three longitudinal keels on the vertex, pronotum, and scutellum, those on the scutellum meeting anteriorly.

Family **Flatidae:** These planthoppers have a wedge-shaped appearance when at rest (Figure 22–51F), and there are usually numerous crossveins in the costal area of the front wings. Most species are either pale green or dark brown. They appear to feed chiefly on vines, shrubs, and trees and are usually found in wooded areas.

Family **Acanaloniidae:** These planthoppers are somewhat similar to the Flatidae, but have a slightly different shape (Figure 22–51E), and they do not have many crossveins in the costal area of the front wings. These planthoppers are usually greenish, with brown markings dorsally.

Family **Issidae:** This is a large and widely distributed group. Most of them are dark-colored and rather stocky in build, and some have short wings and a weevil-like snout (Figure 22–51L).

SUBORDER **Sternorrhyncha:** The members of this suborder are for the most part relatively inactive insects, and some (for example, most scale insects) are quite sedentary. The tarsi are one- or two-segmented, and the antennae (when present) are usually long and filiform. Many members of this suborder are wingless, and some scale insects lack legs and antennae and are not very insectlike in appearance.

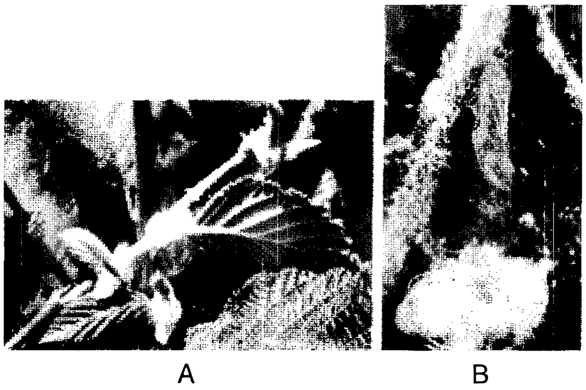

Figure 22–52 The alder psyllid, *Psylla floccosa* (Patch). A, groups of nymphs on alder (these groups form white cottony masses on the twigs, particularly at the base of leaf petioles); B, a newly emerged adult; below the adult is the cast skin of the nymph, still covered with the cottony secretions characteristic of the nymphs of this species.

Family **Psyllidae—Jumping Plantlice or Psyllids:** These insects are small, 2–5 mm long, and usually resemble miniature cicadas in form (Figures 22–52B, 22–53, 22–54B). They are somewhat similar to the aphids, but have strong jumping legs and relatively long antennae. The adults of both sexes are winged, and the beak is short and three-segmented. The nymphs of many species produce large amounts of a white waxy secretion, causing them to superficially resemble the woolly aphids. The jumping plantlice feed on plant juices, and as in the case of most of the Sternorrhyncha, the food-plant relationships are quite specific.

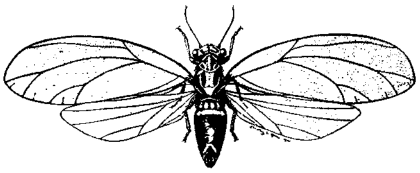

Figure 22–53 The potato psyllid, *Paratrioza cockerelli* (Sulc). (Courtesy of Knowlton and Janes and the Entomological Society of America.)

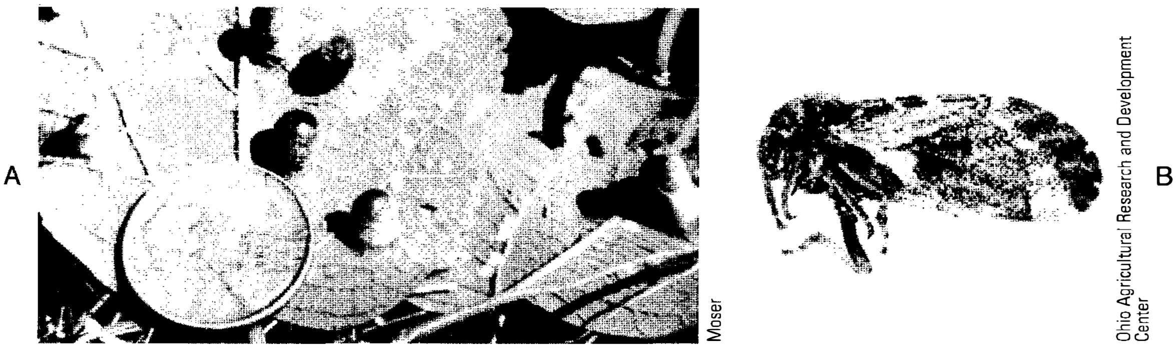

Figure 22–54 A, galls of *Pachypsylla celtidismamma* (Riley) on hackberry; **B**, adult of *Pachypsylla* sp., 20½×.

Two important pest species in this group, the pear psylla, *Cacopsylla pyricola* (Foerster), and the apple sucker, *Cacopsylla mali* (Schmidberger), have been imported from Europe. A western species, the potato or tomato psyllid, *Paratrioza cockerelli* (Sulc) (Figure 22–53), transmits a virus that causes psyllid yellows in potatoes, tomatoes, peppers, and eggplants. This disease reduces yield by dwarfing and discoloring the plant.

The cottony alder psyllid, *Psylla floccosa* (Patch), is a common member of this group in the Northeast. The nymphs feed on alder and produce large amounts of wax, and groups of the nymphs on alder twigs resemble masses of cotton (Figure 22–52A). These insects may sometimes be confused with the woolly alder aphid, *Prociphilus tessellatus* (Fitch). The psyllid is to be found on the alder only during the early part of the summer, but the aphid occurs up until fall. The adults of the cottony alder psyllid (Figure 22–52B) are pale green.

A few of the psyllids are gall-making forms. Species of *Pachypsylla* produce small galls on the leaves of hackberry (Figure 22–54).

Family **Aleyrodidae—Whiteflies**: The whiteflies are minute insects, rarely more than 2 or 3 mm long, that resemble tiny moths. The adults of both sexes are winged, and the wings are covered with a white dust or waxy powder. The adults are usually active whitish insects that feed on leaves.

The metamorphosis of whiteflies is somewhat different from that of most other Hemiptera. The first-instar young are active, but subsequent immature instars are sessile and look like scales. The scalelike covering is a waxy secretion of the insect and has a rather characteristic appearance (Figure 22–55). The wings develop internally during metamorphosis, and the early instars are usually called *larvae*. The next-to-the-last instar is quiescent and is usually called a *pupa*. The wings are everted at the molt of the last larval instar.

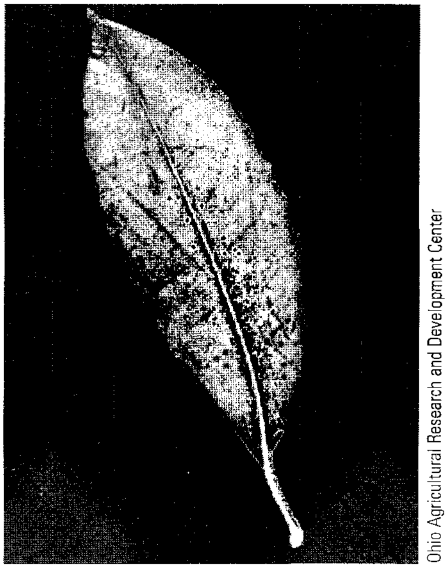

Figure 22–55 "Pupae" of mulberry whiteflies, *Tetraleurodes mori* (Quaintance).

The whiteflies are most abundant in the tropics and subtropics, and the most important pest species in the United States are those that attack citrus trees and greenhouse plants. The damage is done by sucking sap from the leaves. One of the most serious pests in this group is *Aleurocanthus woglumi* Ashby, which attacks citrus trees and is well established in the West Indies and Mexico. An objectionable sooty fungus often grows on the honeydew excreted by whiteflies and interferes with photosynthesis. This fungus is more prevalent in the South and in the tropics than in the North.

Family **Aphididae—Aphids or Plantlice:** The aphids constitute a large group of small, soft-bodied insects that are frequently found in large numbers sucking the sap from the stems or leaves of plants. Such aphid groups often include individuals in all stages of development. The members of this family can usually be recognized by their characteristic pearlike shape, a pair of cornicles at the posterior end of the abdomen, and the fairly long antennae. Winged forms can usually be recognized by the venation and the relative size of the front and hind wings (Figure 22–14C). The wings at rest are generally held vertically above the body.

The cornicles of aphids are tubelike structures arising from the dorsal side of the fifth or sixth abdominal segment. These cornicles secrete a defensive fluid. In some species the body is more or less covered with white waxy fibers, secreted by dermal glands. Aphids also excrete honeydew, from the anus; the honeydew consists mainly of excess sap ingested by the insect, to which are added excess sugars and waste material. This honeydew may be produced in sufficient quantities to cause the surface of objects beneath to become sticky. Honeydew is a favorite food of many ants, and some species, such as the corn root aphid, *Anuraphis maidiradicis* (Forbes), are tended like cows by certain species of ants.

The life cycle of many aphids is rather unusual and complex (Figure 22–56). Most species overwinter in the egg stage, and these eggs hatch in the spring into females that reproduce parthenogenetically and give birth to living young. Several generations may be produced during the season in this way, with only females being produced and the young being born alive. The first generation or two usually consist of wingless individuals, but eventually winged individuals appear. In many species these winged forms migrate to a different host plant, and the reproductive process continues. In the latter part of the season, the aphids migrate back to the original host plant species, and a generation consisting of both males and females appears. The individuals of this bisexual generation mate, and the females lay the eggs, which overwinter.

This method of reproduction can build up enormous populations of aphids in a relatively short time. The aphids would be a great deal more destructive to vegetation were it not for their numerous parasites and predators. The principal parasites of aphids are braconids and chalcidoids, and the most important predators are ladybird beetles, lacewings, and the larvae of some syrphid flies.

This family contains a number of serious pests of cultivated plants. Aphids cause a curling or wilting of the food plant by their feeding, and they serve as vec-

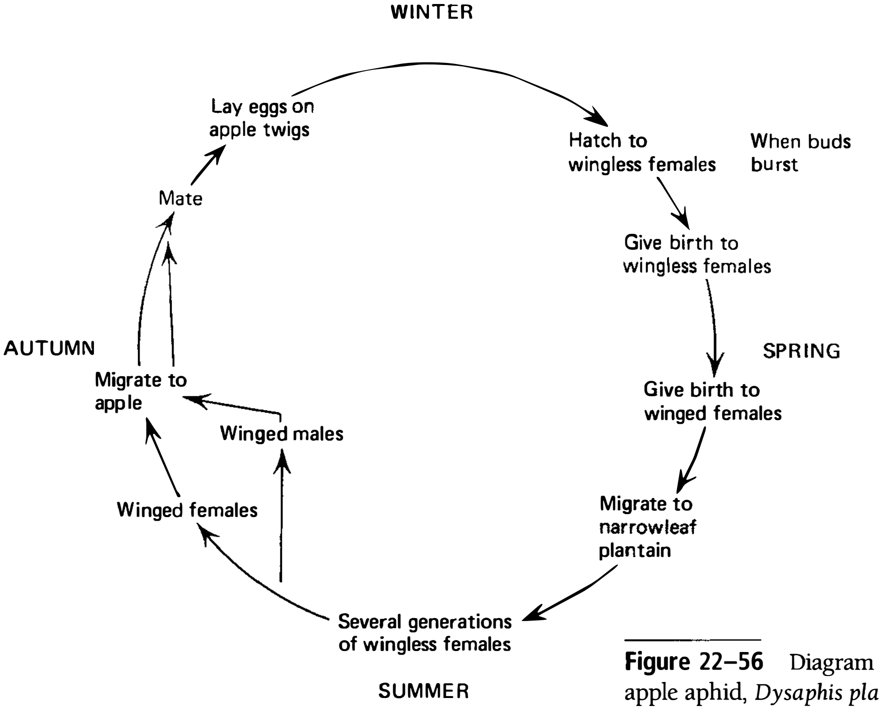

Figure 22–56 Diagram of the life history of the rosy apple aphid, *Dysaphis plantaginea* (Passerini).

tors of a number of important plant diseases. Several diseases are transmitted by aphids, including the mosaics of beans, sugarcane, and cucumbers, by species of *Aphis, Macrosiphum,* and *Myzus*; beet mosaic by *Aphis rumicis* L.; and cabbage ring spot, crucifer mosaic, and potato yellow dwarf by *Myzus persicae* (Sulzer).

The rosy apple aphid, *Dysaphis plantaginea* (Passerini), overwinters on apple and related trees and passes the early summer generations there, then migrates to the narrowleaf plantain as the secondary host. Later in the season it migrates back to apple trees (Figure 22–56). The apple grain aphid, *Rhopalosiphum fitchii* (Sanderson), has apple as its primary host plant and migrates in early summer to grasses, including wheat and oats. Other species of importance are the apple aphid, *Aphis pomi* DeGeer; the cotton aphid (or melon aphid), *A. gossypii* Glover; the potato aphid, *Macrosiphum euphorbiae* (Thomas); the rose aphid, *M. rosae* (L.); the pea aphid, *Acyrthosiphon pisum* (Harris); and the cabbage aphid, *Brevicoryne brassicae* (L.). The largest aphid in the East is the giant bark aphid, *Longistigma caryae* (Harris), 6 mm long, which feeds on hickory, sycamore, and other trees (Figure 22–57A).

The corn root aphid, *Anuraphis maidiradicis* (Forbes), is sometimes a serious pest of corn, and it has an interesting relationship with ants. The eggs of this aphid pass the winter in the nests of field ants, chiefly those in the genus *Lasius*. In the spring, the ants carry the young aphids to the roots of smartweed and other weeds, where the aphids feed. Later in the season, the ants transfer the aphids to the roots of corn. When the aphid eggs are laid in the fall, they are gathered by the ants and stored in their nest for the winter. All during the season, the aphids are tended by the ants, which transfer them from one food plant to another. The ants feed on the honeydew produced by the aphids.

In the woolly and gall-making aphids (Eriosomatinae), the cornicles are reduced or absent and wax glands are abundant. The sexual forms lack mouthparts, and the ovipositing female produces only one egg. Nearly all members of this family alternate between host plants. The primary host (on which the overwintering eggs are laid) is usually a tree or shrub, and the secondary host is a herbaceous plant. These aphids may feed either on the roots of the host plant or on the part of the plant above the ground. Many species produce galls or malformations of the tissues of the primary host, but usually do not produce galls on the secondary host.

The woolly apple aphid, *Eriosoma lanigerum* (Hausmann) (Figure 22–58), is a common and important example of this group. This species feeds principally on the roots and bark and can be recognized by the characteristic woolly masses of wax on its body. These aphids usually overwinter on elm, and the first generations of the season are spent on that host. In early summer, winged forms appear and migrate to apple, hawthorn, and related trees. Later in the season some of these migrate back to elm, where the bisexual generation is produced and the overwintering eggs are laid. Other individuals migrate from the branches of the apple tree to the roots, where they produce gall-like growths. The root-inhabiting forms may remain there a year or more, passing through several generations. This aphid transmits perennial canker.

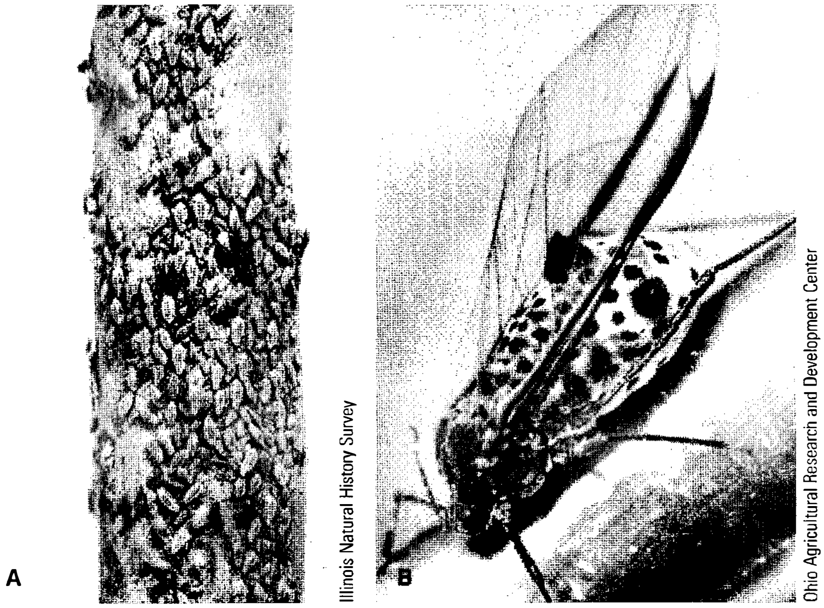

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Figure 22–57 A, a colony of apterous females and nymphs of the giant bark aphid, *Longistigma caryae* (Harris); B, a winged female of the giant willow aphid, *Lachnus salignus* (Gmelin).

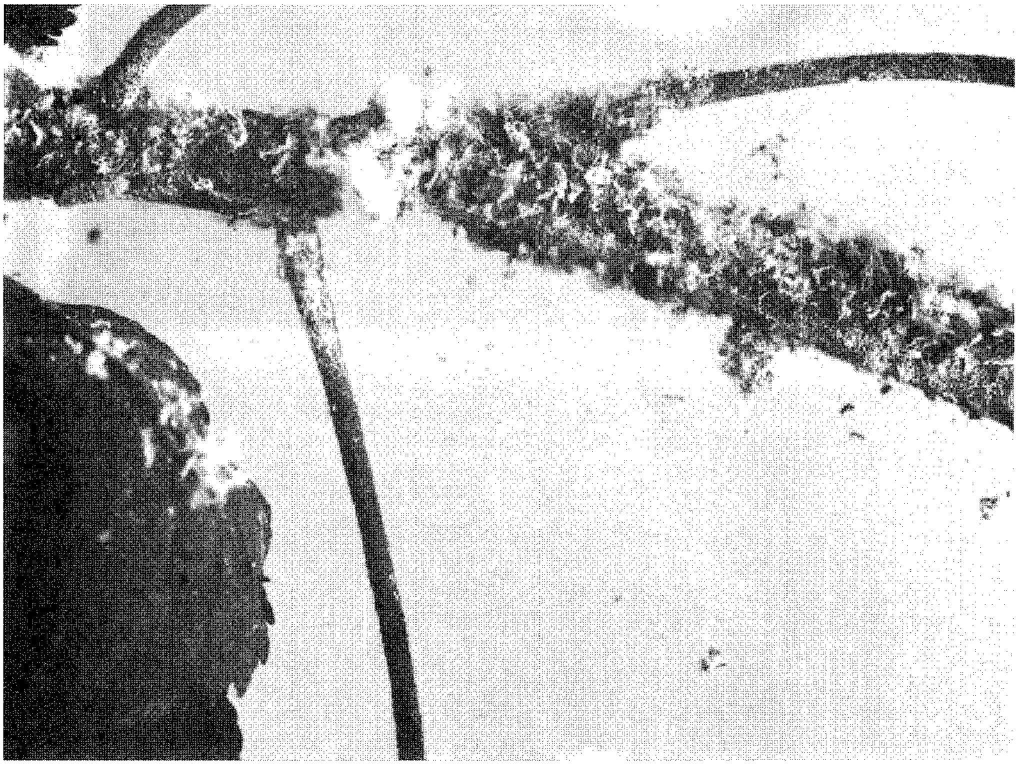

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Figure 22–58 A colony of woolly apple aphids, *Eriosoma lanigerum* (Hausman).

The woolly alder aphid, *Prociphilus tessellatus* (Fitch), is often found in dense masses on the branches of alder and maple. All the generations may be passed on alder, or the species may overwinter on maple and migrate to alder in the summer and then back to maple in the fall, where the sexual forms are produced. The species may overwinter in either the egg or the nymphal stage.

Some of the more common gall-making species in this group are *Colopha ulmicola* (Fitch), which causes the cockscomb gall on elm leaves (Figure 22–59A); *Hormaphis hamamelidis* (Fitch), which causes the cone gall on the leaves of witch hazel; *Hamamelistes spinosus* Shimer, which forms a spiny gall on the flower buds of witch hazel (Figure 22–59B); and *Pemphigus populitransversus* Riley, which forms a marble-shaped gall on the petioles of poplar leaves (Figure 22–59C).

***Family* Adelgidae—Pine and Spruce Aphids:** The members of this group feed only on conifers. They form cone-shaped galls on spruce and, on other hosts, occur as white cottony tufts on the bark, branches, twigs, needles, or cones, depending on the species. Most species alternate between two different conifers in their life history, forming galls only on the primary host tree (spruce). All the females are oviparous. The antennae are five-segmented in the winged forms, four-segmented in the sexual forms, and three-segmented in the wingless, parthenogenetically reproducing females. The body is often covered with waxy threads, and the wings at rest are held rooflike over the body. Cu_1 and Cu_2 in the front wing are separated at the base (Figure 22–12E).

The eastern spruce gall aphid, *Adelges abietis* (L.), is a fairly common species attacking spruce in southeastern Canada and the northeastern part of the United States and forming pineapple-shaped galls on the twigs (Figure 22–60). It has two generations a year, and both generations consist entirely of females. There is no bisexual generation. Both generations live on spruce. Partly grown nymphs pass the winter attached to the base of spruce buds. The nymphs mature into females the following April or May and lay their eggs at the base of the buds. The feeding of these females on the needles of the new shoots causes the needles to swell. The eggs hatch in about a week, and the nymphs settle on the needles that have become swollen by the

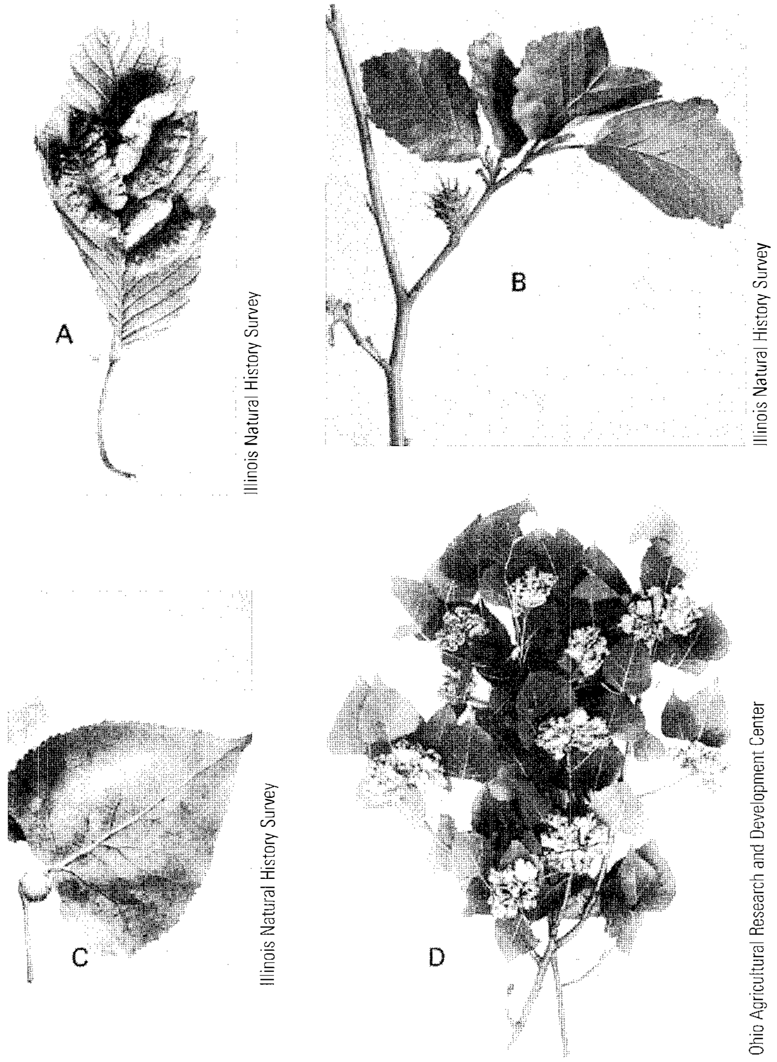

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Figure 22–59 Aphid galls. A, elm cockscomb gall, caused by *Colopha ulmicola* (Fitch); B, spiny bud gall of witch hazel, caused by *Hamamelistes spinosus* Shimer; C, leaf petiole gall of poplar, caused by *Pemphigus populitransversus* Riley; D, vagabond gall of poplar, caused by *Pemphigus vagabundus* Walsh.

mother's feeding. The twig swelling continues and a gall is formed, and the nymphs complete their development in cavities in the gall. Later in the summer, winged females emerge from the galls and lay their eggs on the needles of nearby branches. These eggs hatch, and the nymphs overwinter.

This group contains two genera, *Adelges* and *Pineus*, whose members attack spruce and various other conifers. Perhaps the most important species in the West is the Cooley spruce gall aphid, *Adelges cooleyi* (Gillette), which is also widely distributed in eastern North America and in Europe. The galls of this species on spruce are 12–75 mm long and light green to dark purple, and each chamber in the gall contains from 3 to 30 wingless aphids. The alternate host of this species in the West is Douglas fir, where the insects form white, cottony tufts on new needles, shoots, and developing cones. A severe infestation may cause a heavy shedding of foliage, and the damage, particularly in Christmas tree areas, may be considerable.

***Family* Phylloxeridae—Phylloxerans:** The antennae in this group are three-segmented in all forms, and the wings at rest are held flat over the body. Cu_1 and Cu_2 in the front wing are stalked at the base (Figure 22–12C). These insects do not produce waxy threads, but some species are covered with a waxy powder. The phylloxerans feed on plants other than conifers, and the life history is often very complex.

The grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), is a common and economically important species in this group. This minute form attacks both the leaves and the roots of grape, forming small galls on the leaves (Figure 22–61) and gall-like swellings on the roots. The European grapes are much more suscep-

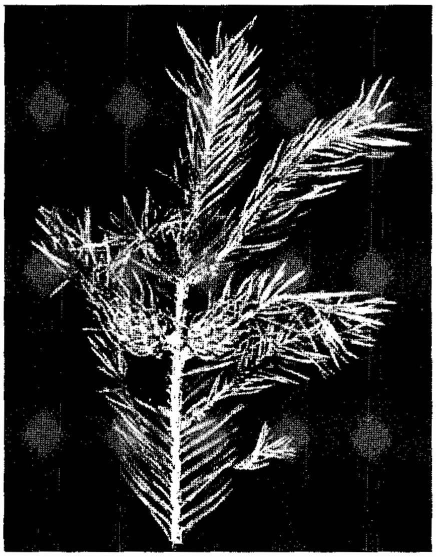

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Figure 22–60 Eastern spruce gall, caused by *Adelges abietus* (L.).

tible to the attacks of this insect than are the native American grapes.

Some of the phylloxerans produce galls on trees. One such species occurring in the East is the hickory gall aphid, *Phylloxera caryaecaulis* (Fitch) (Figure 22–62). These galls reach a diameter of 16–18 mm, and each contains a large number of aphids.

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Figure 22–62 Galls of the hickory gall aphid, *Phylloxera caryaecaulis* (Fitch). A, gall on a hickory leaf; B, two galls cut open to show the insects inside.

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Figure 22–61 Galls on grape leaves caused by the grape phylloxera, *Daktulosphaira vitifoliae* (Fitch).

SUPERFAMILY Coccoidea—Scale Insects: This is a large group and contains forms that are minute and highly specialized. Many are so modified that they look very little like other Hemiptera. Therefore, some authors treat them as a suborder (Coccinea).

The females are wingless and usually legless and sessile, and the males have only a single pair of wings or, rarely, are wingless. The adult males lack mouthparts and do not feed; the abdomen terminates in one (rarely two) long, stylelike process (Figure 22–63A); and the hind wings are reduced to small, halterelike processes that usually terminate in a hooked bristle. The antennae of the female may be lacking or may have up to 11 segments; the antennae of the male have 10–25 segments. Male scale insects look very much like small gnats, but they can usually be recognized by the absence of mouthparts and the presence of a stylelike process at the end of the abdomen.

The development of scale insects varies somewhat in different species, but in most cases it is rather complex. The first-instar nymphs have legs and antennae and are fairly active insects; they are often called "crawlers." After the first molt, the legs and antennae are often lost and the insect becomes sessile, and a waxy or scalelike covering is secreted and covers the body. In the armored scales (Diaspididae), this covering is separated from the body of the insect. The females remain under the scale covering when they become adults to lay eggs or produce live young there. The males develop much like the females, except that the last instar preceding the adult stage is quiescent and is often called a *pupa*. The wings develop externally in the pupa.

Family **Margarodidae—Giant Coccids and Ground Pearls:** This family contains about 45 North American species and includes some of the largest species in the

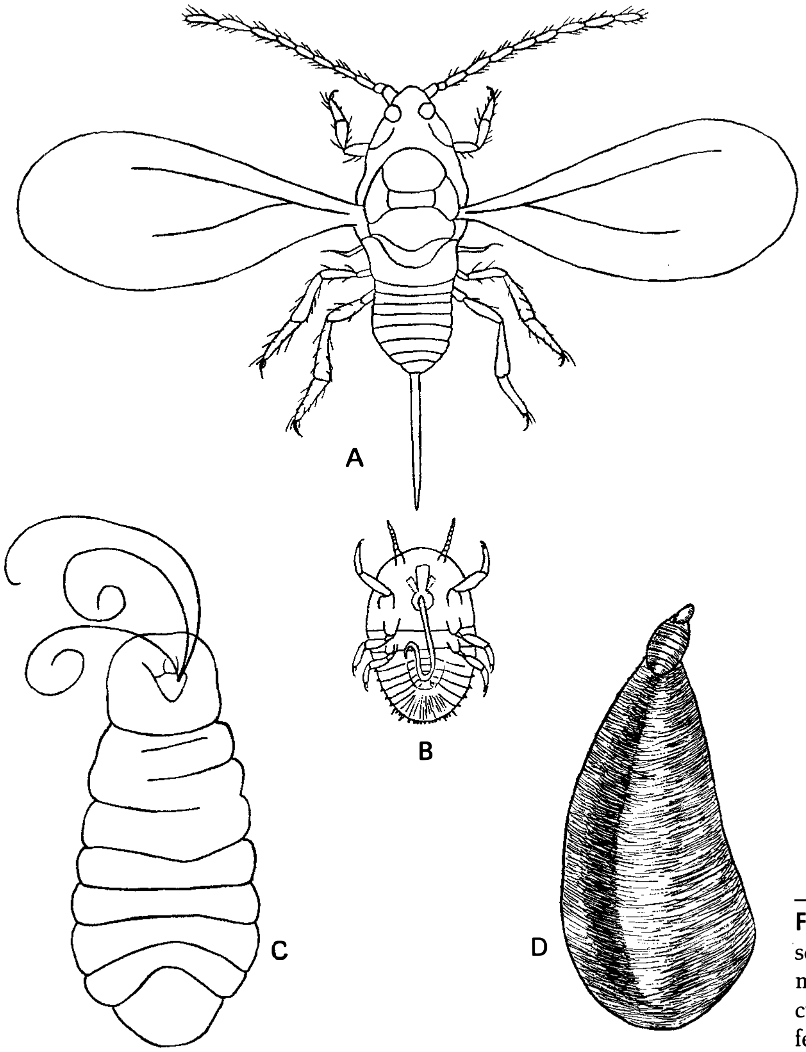

Figure 22–63 Stages of the oystershell scale, *Lepidosaphes ulmi* (L.). A, adult male; B, newly hatched young, or crawler; C, adult female; D, scale of female.

superfamily. Some species of *Llaveia* and *Callipappus* may reach a length of about 25 mm. The name "ground pearls" comes from the pearl-like appearance of the wax cysts of females in the genus *Margarodes*, which live on the roots of plants. The cysts of tropical *Llaveia* species are used in making varnish. The cottony cushion scale, *Icerya purchasi* Maskell, is an important pest of citrus in the West. Several species in the genus *Matsucoccus* are pests of pines.

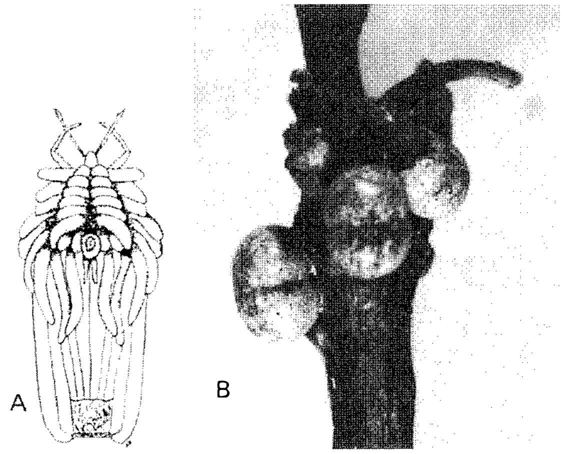

Figure 22–64 A, an ensign scale, *Orthezia solidaginis* (Sanders), female; B, bur oak scale, *Nanokermes pubescens* (Bogue). (A, redrawn from Sanders; B, courtesy of the Ohio Agricultural Research and Development Center.)

Family **Ortheziidae—Ensign scales**: The females in this group are distinctly segmented, elongate-oval, and covered with hard, white, waxy plates (Figure 22–64A). Some carry a white egg sac at the posterior end of the body. These insects may live on almost any part of the host plant, including roots. There are 31 species of ensign scales in the United States, 21 of which are in the genus *Orthezia*. One of these, *O. insignis* Browne, is a common and important greenhouse pest.

Family **Pseudococcidae—Mealybugs**: The name "mealybug" is derived from the mealy or waxy secretions that cover the bodies of these insects. The body of the female is elongate-oval, segmented, and has well-developed legs (Figure 22–65). Some species lay eggs, and others give birth to living young. When eggs are laid, they are placed in loose, cottony wax. Mealybugs may be found on almost any part of the host plant.

This is a large group, with about 240 species in North America. There are several important pest species in this group. The citrus mealybug, *Planococcus citri* (Risso), is a serious pest of citrus and also attacks greenhouse plants. The longtailed mealybug, *Pseudococcus longispinus* (Targioni-Tozzetti), is often found in greenhouses, where it attacks a variety of plants. The obscure mealybug, *Pseudococcus affinis* (Maskell), is a widespread pest on both woody and herbaceous plants.

This family includes the tamarisk manna scale, *Trabutina mannipara* (Ehrenberg), which is believed to have produced the manna mentioned in the Bible. This species feeds on plants in the genus *Tamarix*, and the females excrete large amounts of honeydew. In arid regions the honeydew solidifies on the leaves and accu-

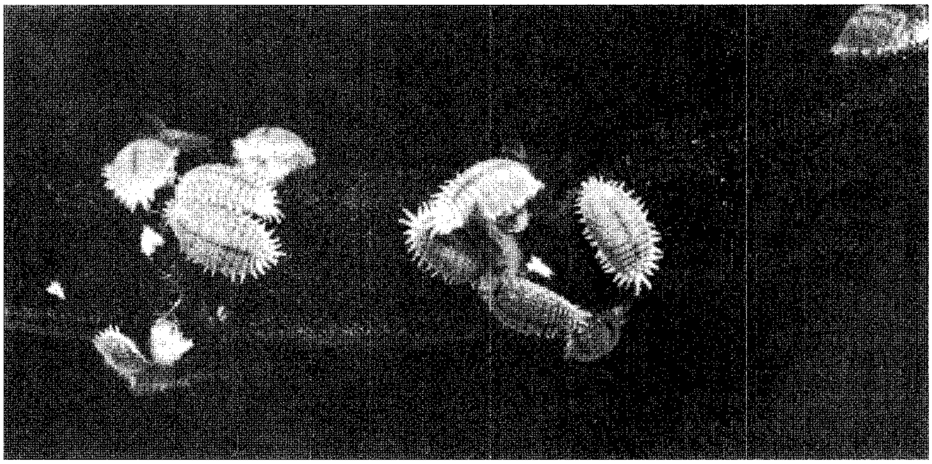

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Figure 22–65 The citrus mealybug, *Planococcus citri* (Risso).

mulates in thick layers to form a sweet, sugarlike material called *manna.*

Family **Eriococcidae—Felt Scales:** These insects are similar to the pseudococcids, but the body is bare or only lightly covered with wax. The female and her eggs are often entirely enclosed in a feltlike sac. This is a widely distributed group, with about 55 species in the United States. The European elm scale, *Gossyparia spuria* (Modeer), is a common pest of elms in North America and Europe. A sooty mold develops on the honeydew secreted by this insect. The azalea bark scale, *Acanthococcus azaleae* (Comstock), is an important pest of azaleas. The oak eriococcin, *Acanthococcus quercus* (Comstock), is a common pest on oaks in North America.

Family **Cryptococcidae—Bark-Crevice Scales:** This family is represented in the United States by two species of *Cryptococcus*, which occur in the northeastern states. They are found in bark crevices of beech and sugar maple.

Family **Kermesidae—Gall-Like Scales:** The females in this group are rounded and resemble small galls (Figure 22–64B). Besides the 13 unplaced and uncertain species, about 22 species occur in the United States, and they are found on the twigs or leaves of oak.

Family **Dactylopiidae—Cochineal Insects:** These insects resemble the mealybugs in appearance and habits. The females are red, broadly oval in shape, and distinctly segmented, and the body is covered with white wax. The group is represented in the United States by three species of *Dactylopius*, which live on cactus (*Opuntia* and *Nopalea*). A Mexican species, *D. coccus* Costa, is an important source of a crimson dye, and is still cultivated in the Canary Islands and in the tropical Americas. Mature females are brushed from the cacti and dried, and the pigments are extracted from their dried bodies. These insects were commercially more important until about 1875, when aniline dyes were introduced.

Family **Asterolecaniidae—Pit Scales:** These insects are called *pit scales* because many of them produce gall-like pits or depressions in the bark of their hosts. This group is a small one, with 17 species in the United States, and they attack a variety of hosts. Some live on the bark, and others live on the leaves of the host.

Family **Cerococcidae—Ornate Pit Scales:** This group is represented in North America by five species of *Cerococcus*, which live on a variety of host plants. *Cerococcus kalmiae* Ferris is occasionally a pest of azaleas and cranberries. The oak wax scale, *C. quercus* Comstock, lives on oak in California and Arizona, and the sugary secretion and excretion in which it is encased was once used as chewing gum by Native Americans.

Family **Lecanodiaspididae—False Pit Scales:** This group is represented in the United States by about five species of *Lecanodiaspis*. Some of these are fairly common and are occasionally pests of azalea, holly, and other ornamentals. They often produce pits and swellings on twigs.

Family **Aclerdidae—Grass Scales:** This is a small family (14 North American species), most of whose members feed on grasses. These scales usually live beneath the leaf sheaths or at the base of the plant, sometimes on the roots. Two North American species feed on Spanish moss, and some tropical species attack orchids.

Family **Coccidae—Soft Scales, Including Wax Scales, and Tortoise Scales:** The females in this group are elongate-oval, usually convex but sometimes flattened, with a hard, smooth exoskeleton or a covering of soft wax. Legs are usually present, and the antennae are either absent or much reduced. The males may be winged or wingless.

This is a large group, with about 105 North American species, a number of which are important pests. The brown soft scale, *Coccus hesperidium* L., and the black scale, *Saissetia oleae* (Olivier), are important pests of citrus in the South. The hemispherical scale, *Saissetia coffeae* (Walker), is a common pest of ferns and other plants in homes and greenhouses. Several species in this group attack shade and fruit trees. The tulip-tree scale, *Toumeyella liriodendri* (Gmelin), is one of the largest scale insects in the United States, the adult female being about 8 mm long. The cottony maple scale, *Pulvinaria innumerabilis* (Rathvon), is a relatively large species (about 6 mm long) whose eggs are laid in a large, cottony mass that protrudes from the end of the scale (Figure 22–66). Many soft scales (Figure 22–67) attack a variety of plants and are often pests in greenhouses.

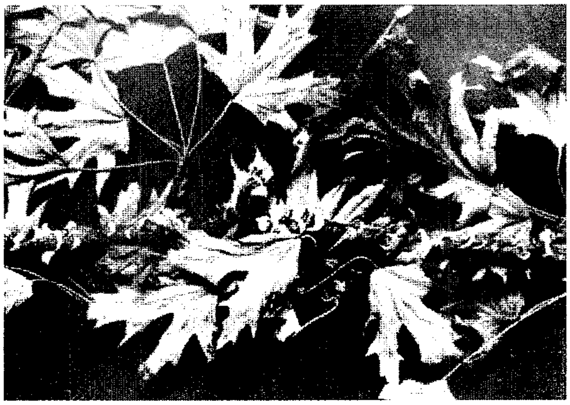

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Figure 22–66 The cottony maple scale, *Pulvinaria innumerabilis* (Rathvon).

Figure 22–67 The terrapin scale, *Mesolecanium nigrofasciatum* (Pergande) (Coccidae).

The Chinese wax scale, *Ericerus pela* Chavannes, is an interesting and important Oriental species. The males secrete large amounts of a pure white wax, which was used in making candles. Wax is also produced by the wax scales of the genus *Ceroplastes*. The Indian wax scale, *C. ceriferus* Anderson, produces a wax that is used for medicinal purposes.

Family **Kerriidae—Lac Scales**: The families in this group are globular in form and legless and live in cells of resin. Seven species of *Tachardiella* occur in the Southwest, where they feed on desert plants. They all produce lac, some of which are highly pigmented.

Most members of this family are tropical or subtropical in distribution, and one, the Indian lac insect, *Laccifer lacca* (Kerr), is of considerable commercial value. It occurs on different plants in Sri Lanka, Taiwan, India, Indochina, and the Philippine Islands. The bodies of the females become covered with heavy exudations of wax or lac and are sometimes so numerous that the twigs are coated with lac to a thickness of 5–15 mm. The twigs are cut and the lac is melted off, refined, and used in the production of shellac and varnishes. About 4 million pounds of this material is harvested annually.

Family **Phoenicococcidae—Date Scales:** This group is represented in the United States by a single species, the red date scale, *Phoenicococcus marlatti* (Cockerell), which occurs on the date palm in the southwestern states. It is usually found at the bases of the leaf petioles or under the fibrous covering of the trunk.

Family **Conchaspididae—False Armored Scales:** Only two species in this group occur in the United States: *Conchaspis angraeci* Cockerell occurs in California and Florida, where it lives on orchids. *Asceloconchaspis milleri* Williams is in southern Florida and feeds on tietongue (*Coccoloba diversifolia* Jacq.). The females are similar to those of the Diaspididae, but they have well-developed legs, and the antennae are four-segmented.

Family **Diaspididae—Armored Scales:** This is the largest family of scale insects (about 310 North American species in 86 genera), and it contains a number of very important pest species. The females are very small and soft-bodied and are concealed under a scale covering that is usually free from the body of the insect underneath. The scale covering is formed of wax secreted by the insect, together with the excretions and cast skins of the early instars. The scales vary in different species. They may be circular or elongate, smooth or rough, and variously colored. The scale covers of the male are usually smaller and more elongate than those of the female. The adult female's body is small, flattened, disklike, and the segmentation is frequently obscure. They lack eyes and legs, and the antennae are absent or vestigial. The males are winged and have well-developed legs and antennae.

Reproduction may be bisexual or parthenogenetic. Some species are oviparous, and others give birth to living young. The eggs are laid under the scale cover. The first-instar young, or crawlers, are active insects and may travel some distance before finding a suitable site to settle. They are able to live several days without food. A species is spread in this crawler stage, either by the locomotion of the crawler itself or by the crawlers being transported by wind or on the feet of birds or by other means. Eventually the crawlers settle down and insert their mouthparts into the host plant. The females remain sessile the remainder of their lives.

These insects injure plants by extracting sap and, when numerous, may kill the plant. The armored scales feed principally on trees and shrubs and may sometimes heavily encrust the twigs or branches. Several species are important pests of orchard and shade trees.

The San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Figure 22–68), is a very serious pest. It first appeared in California about 1880, probably from Asia, and has since spread throughout the United

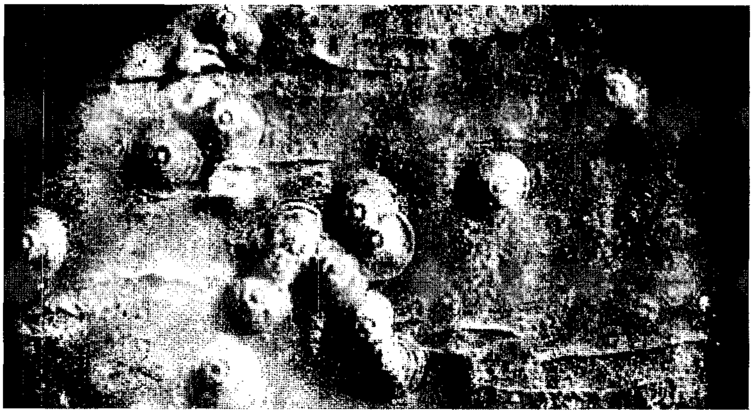

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Figure 22–68 The San Jose scale, *Quadraspidiotus perniciosus* (Comstock).

States. It attacks a number of different trees and shrubs, including orchard trees, shade trees, and ornamental shrubs, and when numerous it may kill the host plant. The scale cover is somewhat circular in shape. This species gives birth to living young.

The oystershell scale, *Lepidosaphes ulmi* (L.), is another economically important species. It is so named because of the shape of its scale (Figure 22–69). This widely distributed species attacks a number of plants, including most fruit trees and many ornamental trees and shrubs. Plants heavily infested are often killed. The oystershell scale lays eggs that overwinter under the scale cover of the female.

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Figure 22–69 The oystershell scale, *Lepidosaphes ulmi* (L.).

A number of other armored scales are somewhat less important than the two just mentioned. The scurfy scale, *Chionaspis furfura* (Fitch), is a common scale with a whitish scale cover that attacks a number of fruit and ornamental trees and shrubs. The rose scale, *Aulacaspis rosae* (Bouché), is a reddish insect with a white scale and attacks various types of berries and roses. Heavily infested plants look as though they had been whitewashed. The pine needle scale, *Chionaspis pinifoliae* (Fitch), is common throughout the United States and Canada on pine, and sometimes attacks other conifers.

Several tropical or subtropical species in this group attack citrus and greenhouse plants. The California red scale, *Aonidiella aurantii* (Maskell), is an important pest of citrus in California. The female has a circular scale cover slightly larger than that of the San Jose scale.

Collecting and Preserving Hemiptera

The aquatic bugs can be collected by means of the aquatic collecting equipment and methods described in Chapter 35. A few aquatic species, particularly water boatmen and giant water bugs, can often be collected at lights. Examine a variety of aquatic habitats, because different species occur in different types of situations. Terrestrial forms can be collected with a net (particularly by sweeping vegetation), at lights, or by examining such specialized habitats as in leaf litter, under bark, and in fungi.

A laboratory squeeze bottle of 70% alcohol with a long exit tube is sometimes useful in capturing active ground-dwelling bugs such as shore bugs. A hit with a squirt of alcohol will slow down the insect so that it can be picked up with forceps.

The methods of collecting and preserving Auchenorrhyncha and Sternorrhyncha vary with the group concerned. The active species are collected and preserved much like other insects, but special techniques are used for such forms as the aphids and scale insects.

Most of the active species are best collected by sweeping. Different species live on different types of plants; to secure a large number of species, collect from as many different types of plants as possible. The smaller hopping species can be removed from the net with an aspirator, or the entire net contents can be stunned and sorted later. Forms that are not too active can be collected from foliage or twigs directly into a killing jar, without using a net. Some of the cicadas, which spend most of their time high in trees, can be collected with a long-handled net. They can be dislodged with a long stick in the hope that they will land within net range, or they can be shot down. A slingshot loaded with sand or fine shot can be used to collect cicadas that are out of reach.

The best type of killing bottle for most Hemiptera is a small vial such as that shown in Figure 35–2, which should be partly filled with small pieces of cleansing tissue or lens paper. Bring along several such vials, because large and heavy-bodied specimens should not be put into the same vial with small and delicate specimens. After specimens have been killed, take them from the vial and place them in pillboxes that are partly filled with cleansing tissue or Cellucotton.

Most Heteroptera are preserved dry on pins or points. Pin the larger specimens through the scutellum, and the smaller specimens through the right hemelytron. In pinning a bug, take care not to destroy structures on the ventral side of the thorax that will be used in identification. Most Heteroptera shorter than 10 mm should be mounted on points. Mount specimens so that the beak, legs, and ventral side of the body are not embedded in glue. The point should not extend beyond the middle of the ventral side of the insect.

Cicadas, the various hoppers, whiteflies, and psyllids are usually mounted dry, on either pins or points. If pinning a larger hopper, pin it through the right wing. Whiteflies and psyllids are sometimes preserved in fluids and mounted on microscope slides for study. Aphids that are pinned or mounted on points usually shrivel. Preserve these insects in fluids, and mount them on microscope slides for detailed study.

It is desirable to mount these insects, particularly the soft-bodied ones, as soon as possible after they are captured. A field catch can be stored in 70 or 75% alcohol until the specimens can be mounted, but alcohol fades some colors. Preserve all nymphs in alcohol.

Scale insects can be preserved in two general ways: The part of the plant containing the scales can be collected, dried, and mounted (pinned or in a Riker mount), or the insects can be specially treated and mounted on a microscope slide. No special techniques are involved in the first method, which is satisfactory if one is interested only in the form of the scale. The insects themselves must be mounted on microscope slides for detailed study. The best way to secure male scale insects is to rear them from colonies found on the host plants. Very few are ever collected with a net.

In mounting a scale insect on a microscope slide, the insect is removed, cleaned, stained, and mounted. Some general suggestions for mounting insects on microscope slides are given in Chapter 35. The following procedures are specifically recommended for mounting scale insects:

1. Place the dry scale insect, or fresh specimens that have been in 70% alcohol for at least 2 hours, in 10% potassium hydroxide and warm at low temperature until the body contents are soft.
2. While the specimen is still in the potassium hydroxide, remove the body contents by making a small hole in the body (at the anterior end or at the side where no taxonomically important characters will be damaged) and pressing the insect with a flat spatula.
3. Transfer the specimen to acetic acid alcohol for 20 minutes or more. Acetic acid alcohol is made by mixing 1 part of acetic acid, 1 part of distilled water, and 4 parts of 95% alcohol by volume.
4. Stain in acid fuchsin for 10 minutes or more as needed. Then transfer to 70% alcohol for 5 to 15 minutes to wash out excess stain.
5. Transfer the specimen to 95% alcohol for 5 to 10 minutes.
6. Transfer the specimen to 100% alcohol for 5 to 10 minutes.
7. Transfer the specimen to clove oil for 10 minutes or more.
8. Mount in Canada balsam.
9. Dry slides for two weeks in a drying oven at 40°C before permanently labelling and studying.

Aphids should be preserved in 80% alcohol and can often be collected from the plant directly into a vial of alcohol. Winged forms are usually necessary for specific identification and should be mounted on microscope slides.

References

Alexander, R. D., and T. E. Moore. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Misc. Publ. Mus. Zool. Univ. Mich. No. 121, 59.

Ben-Dov, Y. 1993. A Systematic Catalogue of the Soft Scale Insects of the World (Homoptera: Coccoidea: Coccidae) with Data on Geographical Distribution, Host Plants, Biology, and Economic Importance. Flora and Fauna Handbook No. 9.Gainesville, FL: Sandhill Crane Press, 536 pp.

Ben-Dov, Y. 1994. A Systematic Catalogue of the Mealybugs of the World (Insecta: Homoptera: Coccoidea: Pseudococcidae, and Putoidae) with Data on Geographical Distribution, Host Plants, Biology, and Economic Importance. Andover, UK: Intercept Limited, 686 pp.

Blatchley, W. S. 1926. Heteroptera or True Bugs of Eastern North America, with Special Reference to the Faunas of Indiana and Florida. Indianapolis: Nature, 1116 pp.

Bobb, M. L. 1974. The insects of Virginia. No. 7. The aquatic and semi-aquatic Hemiptera of Virginia. Va. Polytech. Inst. State Univ. Res. Div. Bull. 87:1–196.

Deitz, L. L. 1975. Classification of the higher categories of the New World treehoppers (Homoptera: Membracidae). N.C. Agr. Expt. Sta. Bull. 225:1–177.

DeLong, D. M. 1948. The leafhoppers, or Cicadellidae, of Illinois (Eurymelinae-Balcluthinae). Ill. Nat. Hist. Surv. Bull. 24(2):91–376.

DeLong, D. M. 1971. The bionomics of leafhoppers. Annu. Rev. Entomol. 16:179–210.

DeLong, D. M., and P. H. Freytag. 1967. Studies of the world Gyponinae (Homoptera, Cicadellidae): A synopsis of the genus *Ponana*. Contrib. Amer. Entomol. Inst. 1(7):1–86.

Doering, K. 1930. Synopsis of North American Cercopidae. J. Kan. Entomol. Soc. 3:53–64, 81–108.

Drake, C. J., and N. T. Davis. 1960. The morphology, phylogeny, and higher classification of the family Tingidae, including the descriptions of a new genus and species of the subfamily Vianaidinae (Hemiptera-Heteroptera). Entomol. Amer. 39:1–100.

Drake, C. J., and F. A. Ruhoff. 1960. Lace-bug genera of the world (Hemiptera: Tingidae). Proc. U.S. Natl. Mus. 122:1–105.

Drake, C. J., and F. A. Ruhoff. 1965. Lacebugs of the world: A catalogue (Hemiptera: Tingidae). Bull. U.S. Natl. Mus. 243:1–634.

Duffels, J. P., and P. A. van der Laan. 1985. Catalogue of the Cicadoidea (Homoptera, Auchenorrhyncha), 1956–1980. The Hague: Junk, 414 pp.

Dybas, H. S., and M. Lloyd. 1974. The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). Ecol. Monogr. 44(3):279–324.

Eastop, V. F., and D. H. R. Lambers. 1976. Survey of the World's Aphids. The Hague: Junk, 574 pp.

Emsley, M. G. 1969. The Schizopteridae (Hemiptera:Heteroptera) with the description of a new species from Trinidad. Mem. Amer. Entomol. Soc. 25:154 pp.

Evans, J. W. 1963. The phylogeny of the Homoptera. Annu. Rev. Entomol. 8:77–94.

Ferris, G. F. 1937–1955. Atlas of the Scale Insects of North America. Stanford, CA: Stanford University Press, 7 vols.

Froeschner, R. C. 1941–1961. Contributions to a synopsis of the Hemiptera of Missouri. Part 1: Scutelleridae, Podopidae, Pentatomidae, Cydnidae, Thyreocoridae. Amer. Midl. Nat. 26(1):122–146 (1941). Part 2: Coreidae, Aradidae, Neididae. Amer. Midl. Nat. 27(3):591–609 (1942). Part 3: Lygaeidae, Pyrrhocoridae, Piesmidae, Tingidae, Enicocephalidae, Phymatidae, Ploiariidae, Reduviidae, Nabidae. Amer. Midl. Nat. 31(3):638–683 (1944). Part 4: Hebridae, Mesoveliidae, Cimicidae, Anthocoridae, Cryptostemmatidae, Isometopidae, Miridae. Amer. Midl. Nat. 42(1):123–188 (1949). Part 5: Hydrometridae, Gerridae, Veliidae, Saldidae, Ochteridae, Gelastocoridae, Naucoridae, Belostomatidae, Nepidae, Notonectidae, Pleidae, Corixidae. Amer. Midl. Nat. 67(1):208–240 (1961).

Froeschner, R. C. 1960. Cydnidae of the Western Hemisphere. Proc. U.S. Natl. Mus. 111:337–680.

Gill, R. J. 1988. The Scale Insects of California: Part 1. The Soft Scales of California. Tech. Series in Agric. Biosyst. & Plant Path., No. 1. Sacramento: California Department of Food and Agriculture, 132 pp.

Gill, R. J. 1993. The Scale Insects of California: Part 2. The Minor Families (Homoptera:Coccoidea): Margarodidae, Ortheziidae, Kerriidae, Asterolecaniidae, Lecanodiaspididae, Cerococcidae, Aclerdidae, Kermesidae, Dactylopiidae, Eriococcidae, and Phoenicococcidae. Tech. Series in Agric. Biosyst. & Plant Path., No. 2. Sacramento: California Department of Food and Agriculture, 241 pp.

Gill, R. J. 1997. The Scale Insects of California: Part 3. The Armoured Scales (Homoptera:Diaspididae). Tech. Series in Agric. Biosyst. & Plant Path., No. 3. Sacramento: California Department of Food and Agriculture, 307 pp.

Gullan, P. J., and M. Kosztarab. 1997. Adaptations in scale insects. Ann. Rev. Entomol. 42:23–50.

Hamilton, K. G. A. 1971. Placement of the genus *Microcentrus* in the Aetalionidae (Homoptera: Cicadelloidea), with a redefinition of the family. J. Georgia Entomol. Soc. 6:229–236.

Hamon, A. B., and M. L. Williams. 1984. The Soft Scales of Florida. Arthropods of Florida and Neighboring Land Areas, 11:1–194.

Harris, K. F., and K. Maramorosch. 1977. Aphids as Virus Vectors. New York: Academic Press, 570 pp.

Hendricks, H., and M. Kosztarab. 1999. Revision of the Tribe Serrolecaniini (Homoptera: Pseudococcidae). New York: de Gruyter, 237 pp.

Henry, T. J. 1997. Phylogenetic analysis of family groups within the infraorder Pentatomomorpha (Hemiptera: Heteroptera), with emphasis on the Lygaeoidea. Ann. Entomol. Soc. Amer. 90:275–301.

Henry, T. J., and R. C. Froeschner (Eds.). 1988. Catalog of the Heteroptera, or True Bugs, of Canada and the Continental United States. Leiden: Brill, 958 pp.

Herring, J. L. 1976. Keys to the genera of Anthocoridae of America north of Mexico, with description of a new genus (Hemiptera: Heteroptera). Fla. Entomol. 59:143–150.

Herring, J. L., and P. D. Ashlock. 1971. A key to the nymphs of the families of Hemiptera (Heteroptera) of America north of Mexico. Fla. Entomol. 54:207–213.

Hoffman, R. L. 1971. The insects of Virginia, No. 4: Shield bugs (Hemiptera; Scutelleroidea; Scutelleridae, Corimelaenidae, Cydnidae, Pentatomidae). Va. Polytech. Inst. State Univ. Res. Div. Bull. 67, 61 pp.

Howell, J. O., and M. L. Williams. 1976. An annotated key to the families of scale insects (Homoptera: Coccoidea) of America, north of Mexico, based on characteristics of the adult female. Ann. Entomol. Soc. Amer. 69:181–189.

Hungerford, H. B. 1948. The Corixidae of the Western Hemisphere. Univ. Kan. Sci. Bull. 32:1–827.

Kennedy, J. S., and H. L. G. Stroyan. 1959. Biology of aphids. Annu. Rev. Entomol. 4:139–160.

Knight, H. H. 1941. The plant bugs or Miridae of Illinois. Ill. Nat. Hist. Surv. Bull. 22(1):1–234.

Kopp, D. D., and T. R. Yonke. 1973–1974. The treehoppers of Missouri. J. Kan. Entomol. Soc.; Part 1, 46:42–64 (1973); Part 2, 46:233–276 (1973); Part 3, 46:375–421 (1973); Part 4, 46:80–130 (1974).

Kosztarab, M. 1982. Homoptera. In S. P. Parker (Ed.), Synopsis and Classification of Living Organisms, pp. 459–470. New York: McGraw-Hill.

Kosztarab, M. 1996. Scale Insects of Northeastern North America: Identification, Biology, and Distribution. Spec. Publ. No. 3. Martinsville: Virginia Museum of Natural History, 650 pp.

Kosztarab, M., and M. P. Kosztarab. 1988. A selected bibliography of the Coccoidea (Homoptera). Third supplement (1970–1985). Blacksburg, VA: Virginia Polytechnic Institute and State University, Agric. Expt. Sta. Bull. 88-1:1–252.

Kosztarab, M., L. B. O'Brien, M. B. Stoetzel, L. L. Dietz, and P. H. Freytag. 1990. Problems and needs in the study of Homoptera in North America In M. Kosztaraband and C. W. Shaefer (Eds), Systematics of the North American Insects and Arachnids: Status and Needs, pp. 119–145. Va. Agric. Expt. Sta. Inform. Ser. 90-1. Blacksburg: Virginia Polytechnic Institute and State University, 247 pp., illus.

Kramer, J. P. 1983. Taxonomic study of the planthopper family Cixiidae in the United States (Homoptera: Fulgoroidea). Trans. Amer. Entomol. Soc. 109:1–58.

Lambdin, P. L., and M. Kosztarab. 1997. Morphology and systematics of the adult females of the genus *Cerococcus* Comstock (Homoptera: Coccoidea: Cerococcidae). Virginia Polytechnic Institute and State University, Res. Div. Bull. 128; 252 pp.

Lambers, D. H. R. 1966. Polymorphism in Aphididae. Annu. Rev. Entomol. 11:47–78.

Lauck, D. R., and A. S. Menke. 1961. The higher classification of the Belostomatidae (Hemiptera). Ann. Entomol. Soc. of Amer, 54:644–657.

Lent, H., and P. Wygodzinsky. 1979. Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' disease. Bull. Amer. Mus. Nat. Hist. 163(3):125–520.

Marshall, D. C., and J. R. Cooley. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. Evolution 54:1313–1325.

Matsuda, R. 1977. The Aradidae of Canada (Hemiptera: Aradidae). The Insects and Arachnids of Canada. Part 3. Ottawa: Canadian Government Publishing Centre, 116 pp.

McKenzie, H. L. 1967. The Mealybugs of California. Berkeley: University of California Press, 525 pp.

McPherson, J. E. 1982. The Pentatomoidea (Hemiptera) of Northeastern North America. Carbondale: Southern Illinois University Press, 241 pp.

Miller, D. R., and M. Kosztarab. 1979. Recent advances in the study of scale insects. Ann. Rev. Entomol. 24:1–27.

Moore, T. E. 1966. The cicadas of Michigan (Homoptera: Cicadidae). Pap. Mich. Acad. Sci. 51:75–96.

Moore, T. E. 1973. Acoustical behavior of insects. In V. J. Tipton (Ed.), Syllabus, Slides and Cassettes for an Introductory Course (Entomological Society of America), pp. 310–323. Provo, UT: Brigham Young University Press.

Moore, T. E. 1993. Accoustic signals and speciation in cicadas (Insecta: Homoptera: Cicadidae). In D. R. Lees and D. Edwards (Eds.), Evolutionary Patterns and Processes, pp. 269–284. Linnaean Society Symposium No. 14.London: Academic Press.

Oman, P. W., W. J. Knight, and M. W. Nielsen. 1990. Leafhoppers (Cicadellidae): A Bibliography, Generic Checklist and Index to the World Literature 1956–1985. Wallingford, UK: CAB International, 368 pp.

Ossiannilsson, F. 1949. Insect drummers: A study of the morphology and function of the sound-producing organs of Swedish Homoptera Auchenorrhyncha. Opusc. Entomol. Suppl. 10:1–146.

Polhemus, J. T. 1985. Shore Bugs (Heteroptera:Hemiptera: Saldidae). A World Overview and Taxonomy of Middle American Forms. Englewood, CO: The Different Drummer, 252 pp.

Putchkov, V. G., and P. V. Putchkov. 1985. A Catalog of Assassin Bug Genera of the World (Heteroptera, Reduviidae). Kiev: published by the authors, 137 pp.

Russell, L. M., M. Kosztarab, and M. P. Kosztarab. 1974. A Selected Bibliography of the Coccoidea. Second Suppl., Misc. Publ. 1281. Washington, DC: U.S. Department of Agriculture, 122 pp.

Schaefer, C. W. 1964. The morphology and higher classification of the Coreoidea (Hemiptera-Heteroptera), Parts 1 and 2. Ann. Entomol. Soc. Amer. 57:670–684.

Schaefer, C. W. 1965. The morphology and higher classification of the Coreoidea (Hemiptera-Heteroptera). Part 3. The families Rhopalidae, Alydidae, and Coreidae. Misc. Publ. Entomol. Soc. Amer. 5(1):1–76.

Schaefer, C. W., and M. Kosztarab. 1991. Systematics of insects and arachnids: Status, problems, and needs in North America. Amer. Entomologist 37:211–216.

Schuh, R. T. 1986. The influence of cladistics on heteropteran classification. Annu. Rev. Entomol. 31: 67–93.

Schuh, R. T. 1995. Plant Bugs of the World (Insecta): Heteroptera: Miridae). New York: New York Entomological Society, 1329 pp.

Schuh, R. T., B. Galil, and J. T. Polhemus. 1987. Catalog and bibliography of Leptopodomorpha (Heteroptera). Bull. Amer. Mus. Nat. Hist. 185:243–406.

Schuh, R. T., and J. A. Slater. 1995. True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History. Ithaca, NY: Comstock, Cornell University Press, 336 pp.

Schuh, R. T., and J. A. Slater. 1995. True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History. Ithaca, NY: Cornell University Press, 336 pp.

Schuh, R. T., and P. Štys. 1991. Phylogenetic analysis of cimicomorphan family relationships (Heteroptera). J. N.Y. Entomol. Soc. 99:298–350.

Shaw, K. C., A. Vargo, and O. V. Carlson. 1974. Sounds and associated behavior of *Empoasca* (Homoptera: Cicadellidae). J. Kan. Entomol. Soc. 47:284–307.

Slater, J. A. 1964. A Catalogue of the Lygaeidae of the World, vols. 1 and 2. Storrs: University of Connecticut, 1688 pp.

Slater, J. A. 1982. Hemiptera. In S Parker (Ed.), Synopsis and Classification of Living Organisms, pp. 417–447. New York: McGraw-Hill.

Slater, J. A., and R. M. Baranowski. 1978. How to Know the True Bugs. Dubuque, IA: William C Brown, 256 pp.

Slater, J. A., and J. O'Donnell. 1995. A catalogue of the Lygaeidae of the world (1960–1994). J. N.Y. Entomol. Soc., 410 pp.

Smith, C. F. 1972. Bibliography of the Aphididae of the world. N.C. Agr. Expt. Sta. Tech. Bull. 216:1–717 pp.

Staddon, B. W. 1979. The scent glands of Heteroptera. Advances in Insect Physiology, 14:351–418.

Štys, P. 1989. Phylogenetic systematics of the most primitive true bugs (Heteroptera: Enicocephalomorpha, Dipsocoromoropha). Prace Slov. Entomol. Spol. SAV, Bratislava 8:69–85.

Štys, P., and A. Jansson. 1988. Check-list of recent family-group names of Nepomorpha (Heteroptera) of the world. Acta Entomol. Fenn. 50:1–44.

Štys, P., and I. Kerzhner. 1975. The rank and nomenclature of higher taxa in recent Heteroptera. Acta Entomol. Bohemoslovaca 72:64–79.

Sweet, M. H. 1960. The seed bugs: A contribution to the feeding habits of the Lygaeidae (Hemiptera-Heteroptera). Ann. Entomol. Soc. Amer. 53:317–321.

Usinger, R. L. 1943. A revised classification of the Reduvoidea with a new subfamily from South America (Hemiptera). Ann. Entomol. Soc. Amer. 36:602–618.

Usinger, R. L. 1956. Aquatic Hemiptera. In R. L. Usinger (Ed.), Aquatic Insects of California, with Keys to North American Genera and California Species, pp. 182–228. Berkeley: University of California Press, illus.

Usinger, R. L. 1966. Monograph of the Cimicidae (Hemiptera-Heteroptera). Thomas Say Foundation Publ. 7:1–585.

Usinger, R. L., and R. Matsuda. 1959. Classification of the Aradidae (Hemiptera: Heteroptera). London: British Museum (Natural History), 410 pp.

Wade, V. 1966. General catalogue of the Homoptera: Species index of the Membracoidea and fossil Homoptera (Homoptera: Auchenorrhyncha). A supplement to fascicle 1, Membracidae of the general catalogue of the Homoptera. N.C. Agr. Expt. Sta. Pap. No. 2160(2); 40 pp.

Way, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. Annu. Rev. Entomol. 8:307–344.

Wheeler, A. G., Jr. 2001. Biology of the Plant Bugs. Ithaca, NY: Cornell University Press, 507 pp.

Wheeler, A. G., Jr., and T. J. Henry. 1992. A Synthesis of the Holarctic Miridae (Heteroptera): Distribution, Biology, and Origin, with Emphasis on North America. Lanham, MD: The Thomas Say Foundation, Entomological Society of America, 282 pp.

Wheeler, W. C.. R. T. Schuh, and R. Bang. 1993. Cladistic relationships among higher groups of Heteroptera: Congruence between morphological and molecular data sets. Entomol. Scand. 24:121–137.

Williams, M. L., and M. Kosztarab. 1972. Morphology and systematics of the Coccidae of Virginia, with notes on their biology (Homoptera: Coccoidea). Va. Polytech. Inst. State Univ. Res. Div. Bull. 74, 215 pp.

Wygodzinsky, P. 1966. A monograph of the Emesinae (Reduviidae: Hemiptera). Bull. Amer. Mus. Nat. Hist.133, 614 pp.

Wygodzinsky, P., and K. Schmidt. 1991. Revision of the New World Enicocephalomorpha (Heteroptera). Bull. American Mus. Nat. Hist. 200, 165 pp.

Young, D. A. 1952. A reclassification of western hemisphere Typhlocybinae (Homoptera, Cicadellidae). Univ. Kan. Sci. Bull. 35:3–217.

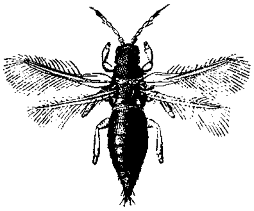
Young, D. A. 1968. Taxonomic study of the Cicadellinae (Homoptera: Cicadellidae). Part 1: Proconiini. Smithson. Inst. Bull. 261, 287 pp.

Young, D. A. 1977. Taxonomic study of the Cicadellinae (Homoptera: Cicadellidae). Part 2: New World Cicadellini and the genus *Cicadella*. N.C. Agr. Exp. Sta. Bull., Raleigh, N. C. 235, 1135 pp.

23

Order Thysanoptera[1,2]

Thrips



The thrips are minute, slender-bodied insects 0.5 to 5.0 mm long (some tropical species are nearly 13 mm long). Wings may be present or absent. When fully developed, the four wings are very long and narrow, with few or no veins, and fringed with long hairs. The fringe of hairs on the wings gives the order its name.

The mouthparts (Figure 23–1) are of the sucking type, and the proboscis is a stout, conical, asymmetrical structure located posteriorly on the ventral surface of the head. The labrum forms the front of the proboscis; the basal portions of the maxillae form the sides; and the labium forms the rear. There are three stylets: one mandible (the left one; the right mandible is vestigial) and the laciniae of the two maxillae. Both maxillary and labial palps are present, but short. The hypopharynx is a small median lobe in the proboscis. The mouthparts of thrips have been described as "punch and suck": The mandible is used to break up the plant cells, and the two maxillary stylets are joined to form a tube through which the plant liquids or fungal spore are sucked and ingested (Heming 1993, Kirk 1997). The food is generally ingested in liquid form, but minute spores are also sometimes ingested.

The antennae are short and four- to nine-segmented. The tarsi are one- or two-segmented, with one or two claws, and are bladderlike at the tip. An ovipositor is present in some thrips. In others, the tip of the abdomen is tubular and an ovipositor is lacking.

The metamorphosis of thrips is somewhat intermediate between simple and complete (Figure 23–2). The first two instars have no wings externally and are usually called *larvae*. In at least some cases, the wings are developing internally during these two instars. In the suborder Terebrantia, the third and fourth instars (only the third instar in *Franklinothrips*) are inactive, do not feed, and have external wings; the third instar is called the ***propupa***, and the fourth the ***pupa***. The pupa is sometimes enclosed in a cocoon. In the suborder Tubulifera, the third instar propupa (without external wings) is followed by two "pupal" instars, the fourth and the fifth. The stage following the pupa is the adult. This type of metamorphosis resembles simple metamorphosis in that more than one preadult instar (except in *Franklinothrips*) has external wings. It resembles complete metamorphosis in that at least some of the wing development is internal, and there is a quiescent (pupal) instar preceding the adult.

The two sexes of thrips are similar in appearance, but the males are usually smaller. Parthenogenesis occurs in many species. Those thrips that have an ovipositor usually insert their eggs in plant tissues. The thrips that lack an ovipositor usually lay their eggs in crevices or under bark. Young thrips are relatively inactive. Generally there are several generations a year.

A great many of the thrips are plant feeders, attacking flowers, leaves, fruits, twigs, or buds. They feed on a wide variety of plants. They are particularly abundant in the flower heads of daisies and dandelions. They destroy plant cells by their feeding, and some species act as vectors of plant disease. Many species are serious pests of cultivated plants. A few thrips feed on fungus spores, and a few are predaceous on other small arthropods. These insects sometimes occur in enormous numbers, and a few species may bite people.

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[1] Thysanoptera: *thysano*, fringe; *ptera*, wings.

[2] This chapter was edited by Steve Nakahara.

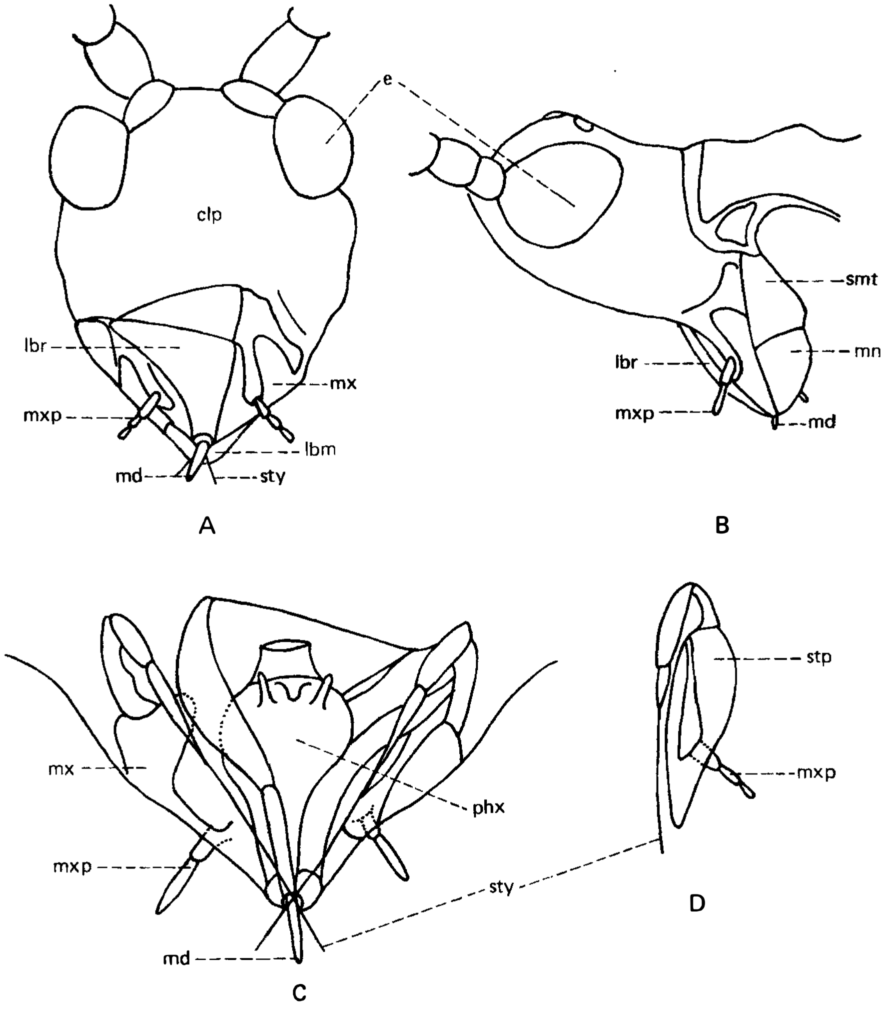


Figure 23–1 Mouthparts of a thrips. A, head, ventro-anterior view; B, head, lateral view; C, mouthparts, posterior view; D, a maxilla. *clp*, clypeus; *e*, compound eye; *lbm*, labium; *lbr*, labrum; *md*, left mandible; *mn*, mentum; *mx*, maxilla; *mxp*, maxillary palp; *phx*, pharynx; *smt*, submentum; *stp*, stipes; *sty*, maxillary stylet. (Redrawn from Peterson, 1915.)

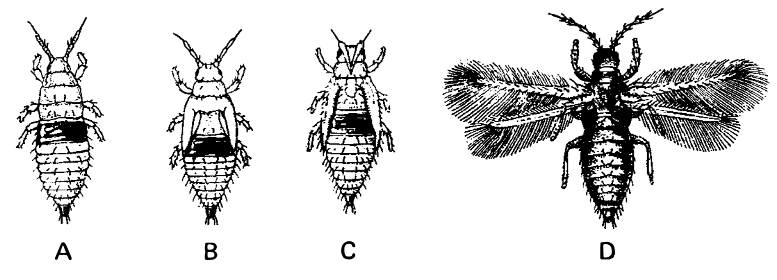


Figure 23–2 The redbanded thrips, *Selenothrips rubrocinctus* (Giard) (Thripidae). A, full-grown larva; B, prepupa; C, pupa; D, adult. (Courtesy of USDA.)

Classification of the Thysanoptera

This order is divided into two suborders, the Terebrantia and the Tubulifera. The Terebrantia currently consist of seven families. They have the last abdominal segment more or less conical or rounded; the female has an ovipositor; the fore wings have veins and setae, the fringe cilia arise from basal sockets, and the surface normally has numerous microtrichia. The Tubulifera currently consists of two families. They have a tubular last abdominal segment; the females lack an ovipositor, and their distal abdominal segments are shaped like those of males; the fore wings lack veins and setae except on the base, the fringe cilia lack basal sockets, and the surface is bare of microtrichia. Seven families of thrips occur in North America: one in the Tubulifera and six in the Terebrantia. The families in the Terebrantia are separated largely by characters of the antennae, particularly the number of antennal segments and the nature of the sensoria on the third and fourth segments. These sensoria are in the form of protruding simple or forked sense cones; or are flat and circular, or oval, elongate, and oriented either longitudinally or transversely near the apex.

Suborder Tubulifera
    Phlaeothripidae
Suborder Terebrantia
    Adiheterothripidae
    Aeolothripidae
    Fauriellidae
    Merothripidae
    Heterothripidae
    Thripidae

Key to the Families of Thysanoptera

1.	Last abdominal segment tubular (Figures 23–3C, 23–4C), female without an ovipositor; front wings, if present, lack longitudinal veins and setae except at base, surface bare of microtrichia, fringe cilia without basal sockets (suborder Tubulifera)	**Phlaeothripidae**	p. 339
1′.	Last abdominal segment conical or rounded apically (Figures 23–3A,B, 23–4A,B,D–G), divided ventrally; female with ovipositor (Figure 23–3A,B); front wings, if present, with longitudinal veins and setae, surface usually with microtrichia, fringe cilia with basal sockets (suborder Terebrantia)	2	
2(1).	Antennal segments 3 and 4 each with a conical, simple or forked sense cone (Figures 23–5D,E, scn; 23–6B); ovipositor curved upward (Figure 23–3B)	3	
2′.	Antennal segments 3 and 4 with sensoria not protruding, flat (Figures 23–5A–C, sa; 23–6A); ovipositor curved upward or downward (Figure 23–3A)	4	

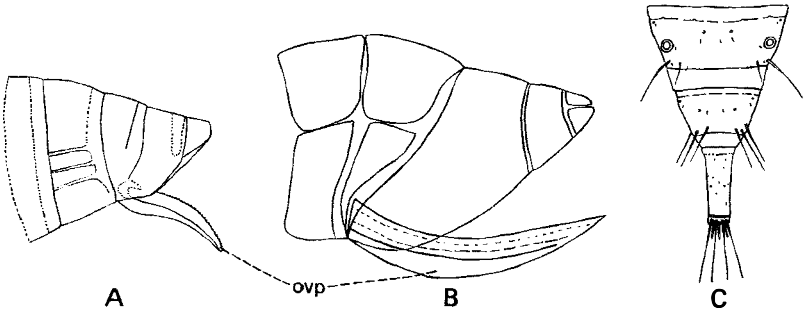


Figure 23–3 Abdominal structures of Thysanoptera. A, apex of abdomen of the pear thrips, *Taeniothrips inconsequens* (Uzel) (Thripidae), lateral view, showing the decurved ovipositor; B, apex of abdomen of *Melanothrips* (Aeolothripidae), lateral view, showing the up-curved ovipositor; C, apex of abdomen of *Haplothrips hispanicus* Priesner (Phlaeothripidae), dorsal view. *ovp*, ovipositor. (Modified from Pesson.)

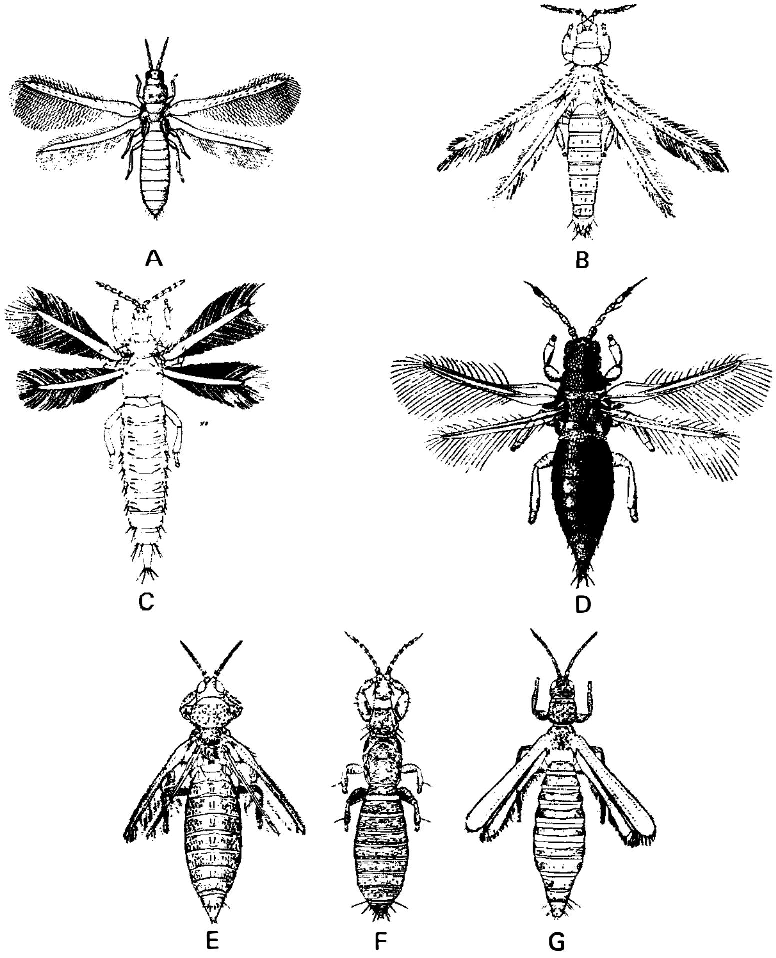


Figure 23–4 Thrips. A, gladiolus thrips, *Taeniothrips simplex* (Morison) (Thripidae); B, pear thrips, *Taeniothrips inconsequens* (Uzel) (Thripidae); C, lily bulb thrips, *Liothrips vaneeckei* Priesner (Phlaeothripidae); D, greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouche) (Thripidae); E, *Heterothrips salicis* (Shull) (Heterothripidae); F, a large-legged thrips, *Merothrips morgani* Hood (Merothripidae); G, a banded thrips, *Stomatothrips crawfordi* Stannard (Aeolothripidae). (A, courtesy of the Utah Agricultural Experiment Station; B, courtesy of Bailey and the Univeristy of California Experiment Station; C, courtesy of Bailey and the California Department of Agriculture; D, courtesy of USDA; E–G, courtesy of Stannard and the Illinois Natural History Survey.)

3(2).	Antennae with segments 3 and 4 each with a conical sense cone (Figure 23–6B), 9-segmented	Adiheterothripidae	p. 338
3′.	Antennae with segments 3 and 4 each with a slender, simple or forked sense cone, 6- to 9-segmented (Figures 23–5D,E)	Thripidae	p. 338
4(2′).	Antennae segments 3 and 4 each with an apical row or band of small sensoria encircling segment (Figure 23–5C, sa)	Heterothripidae	p. 338
4′.	Antennal segments 3 and 4 without a row or band of small sensoria	5	
5(4′).	Antenna 8-segmented, segments 3 and 4 with rather large, apical, tympanum-like sensoria (Figure 23–5A, sa); pronotum with longitudinal suture on each side; ovipositor reduced; abdominal segment 10 with pair of trichobothria (Figure 23–6C)	Merothripidae	p. 338
5′.	Antenna 9-segmented, segments 3 and 4 with sensoria oval, elongate longitudinally or transverse near apex; pronotum without longitudinal lateral sutures; ovipositor well developed, with teeth; abdominal segment 10 with or without small trichobothria	6	

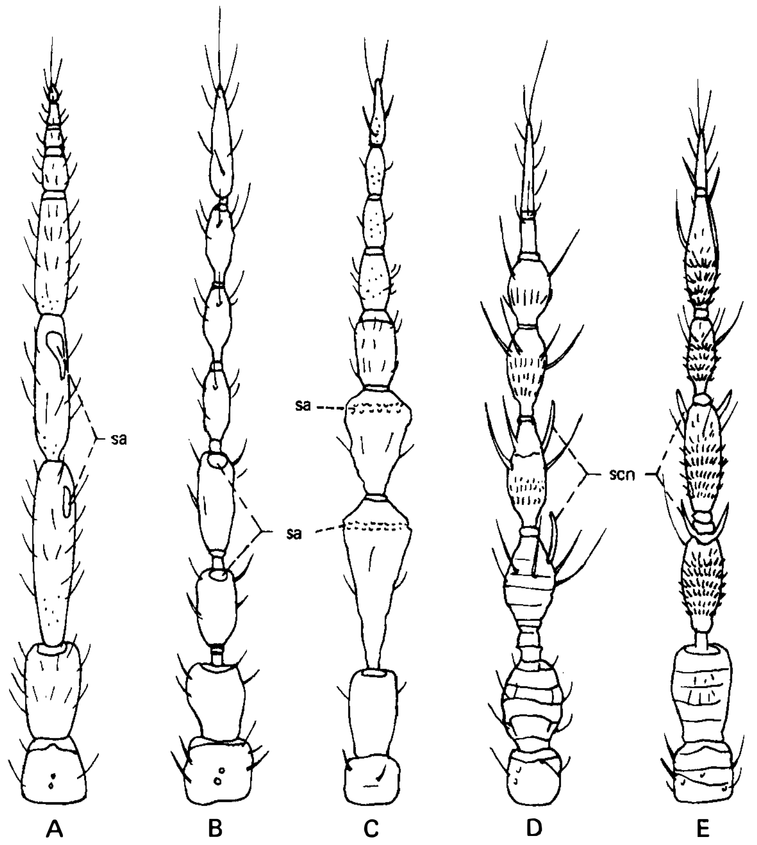


Figure 23–5 Antennae of Thysanoptera. A, *Aeolothrips* (Aeolothripidae); B, *Merothrips* (Merothripidae); C, *Heterothrips* (Heterothripidae); D, *Caliothrips* (Thripidae); E, *Thrips* (Thripidae). *sa*, sensoria; *scn*, sense cone. (Redrawn from Stannard, courtesy of the Illinois Natural History Survey.)

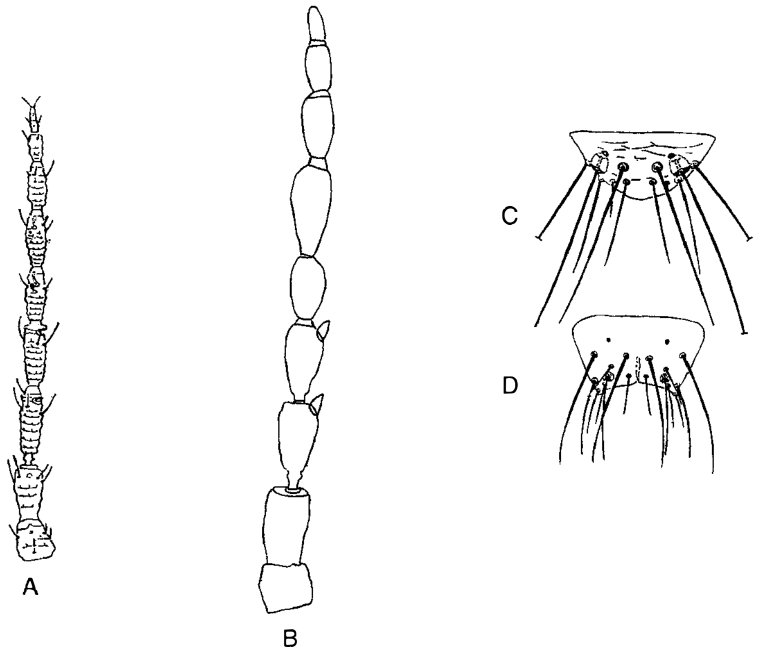


Figure 23–6 Characters of Thysanoptera. A, antenna of *Parrellathrips ullmanae* Mound and Marullo (Fauriellidae); B, antenna of *Oligothrips oreios* Moulton (Adiheterothripidae); C, tergite X of *Merothrips* (Merothripidae); D, tergite X of *Melanthrips* (Aeolothripidae). (A, courtesy of New York Entomological Society; B, courtesy of University of California Press; C, D, courtesy of The Linnean Society of London.)

6(5′).	Fore wings broad, tips rounded; sensoria on antennal segments 3 and 4 oval, elongate longitudinally, or linear and either transverse or oblique near apex (Figures 23–5A, sa); abdominal tergite 10 with pair of small trichobothria; ovipositor curved upward (Figure 23–3B)	Aeolothripidae	p. 338
6′.	Fore wings pointed apically; sensoria on antennal segments 3 and 4 transverse near apex (Figure 23–6A); abdominal tergite 10 without trichobothria; ovipositor curved downward	**Fauriellidae**	p. 338

***Family* Adiheterothripidae:** Several members of this small family were formerly assigned to the Heterothripidae. The two species in North America are distinguished from other families by antennal segments 3 and 4 having a conical sense cone (Figure 23–6B). *Oligothrips oreios* Moulton occurs in blossoms of madrone and manzanita in California and Oregon; *Heratythrips sauli* Mound and Marullo was recently discovered in California.

***Family* Aeolothripidae:** The fore wings in this group are relatively broad (Figure 23–4G), with two longitudinal veins extending from the base of the wing nearly to the tip, and usually with several crossveins. The adults are dark, and often the wings are banded crosswise or longitudinally. There are about 62 nominal species in North America. Most belong in the genus *Aeolothrips*, which includes several predatory species. The most common species in this group, *Aeolothrips fasciatus* (L.), is about 1.6 mm long, dark brown, with three white bands on the fore wings. The larvae are yellowish, shading into orange posteriorly. This species occurs on various plants and is often common in the flower heads of clover. It feeds on other thrips, aphids, mites, and other small insects. It is widely distributed in North America and Europe.

***Family* Fauriellidae:** A recently described species from California, *Parrellathrips ullmanae* Mound and Marullo, taken from canyon silktassel, *Garrya veatchii* Kellogg (Garryaceae), is the only representative in North America of this small disjunct family. In total, the group consists of only five species in four genera. This family is distinguished from other families in North America by the 9-segmented antennae with numerous microtrichia on most segments, a transverse sensoria near the apex of segments 3 and 4 (Figure 23–6A), the fore wing is pointed at the apex, and the ovipositor is curved downward.

***Family* Merothripidae:** The members of this group may be recognized by the sensoria on the apex of antennal segments 3 and 4, which is tympanum-like and usually rather large, a pair of trichobothria on abdominal segment 10, two longitudinal sutures on the pronotum, the large fore and hind femora, and the frequent presence of a hooklike process on the inner apex of the fore tibia. A common species, *Merothrips morgani* Hood (Figure 23–4F), occurs in the eastern United States under bark, in debris, and in fungi. *Merothrips floridensis* Watson also occurs in similar habitats in the eastern and southern states and in other countries.

***Family* Heterothripidae:** This family is known only from the Western Hemisphere, and only one genus, *Heterothrips*, occurs in North America (Figure 23–4E). The adults are usually dark, the abdomen has many microtrichia on the abdominal segments, the fore wing has two complete rows of veinal setae, and the sensoria on antennal segments 3 and 4 are small and arranged in a row or band encircling the apex of the segment. Several species of *Heterothrips* occur on trees (buckeye, oak, and willow) and flowers (azalea, wild rose, and jack-in-the-pulpit) and in the buds of wild grape.

***Family* Thripidae—Common Thrips:** This family is the largest in the Terebrantia in North America and contains most of the species that are of economic importance. The wings are narrower than in the Aeolothripidae and are more pointed at the tip. The antennae are six- to nine-segmented, and segments 3 and 4 each have a protruding, simple or forked sense cone. Most species are macropterous, but may also have apterous or brachypterous forms. Several species are predominantly apterous or brachypterous. Most species feed primarily on plants. Members of the genus *Scolothrips* are predaceous, and a few species in other genera are occasionally predaceous.

The pear thrips, *Taeniothrips inconsequens* (Uzel) (Figure 23–4B), attacks the buds, blossoms, young leaves, and fruits of pears, plums, cherries, and other plants. The adults are brown with pale wings, 1.2 to 1.3 mm long, and have a distinctive small claw at the tip of the fore tarsus. This species has a single generation a year and overwinters as a pupa and adult in the soil. The adults emerge in early spring, feed, then oviposit on the petioles of leaves and fruits. The young feed until about June, when they drop to the ground and burrow into the soil to pupate. This species occurs in the western coastal states and British Columbia, the northeastern states and south to Virginia, and in the Great Lakes states and provinces. *Thrips calcaratus* Uzel is another invasive thrips with a brown coloration, fore tarsal tooth, and life cycle all similar to that of the pear thrips. This thrips damages native basswood in the Great Lakes area of Wisconsin and Minnesota, and is found eastward to Vermont.

The gladiolus thrips, *Taeniothrips simplex* (Morison), is a serious pest of gladiolus, injuring the leaves and greatly reducing the size, development, and color of the flowers. It has a brown body, fore wing, and antenna, except for a yellow segment 3 (Figure 23–4A). The onion thrips, *Thrips tabaci* Lindeman, is a widely distributed species that attacks onions, beans, and many other plants. It is a pale yellowish or brownish insect 1.0 to 1.2 mm long. It vectors the tospovirus causing tomato spotted wilt disease in tomatoes and other plants. *Heliothrips haemorrhoidalis* (Bouché) (Figure 23–4D) is a tropical species that occurs outdoors in the warmer parts of the world and is a serious pest in greenhouses in the North. The male of this species is very rare. The flower thrips, *Frankliniella tritici* (Fitch), is a common and polyphagous species in the eastern half of the United States, and is a pest of fruit trees, flowers, grains, and truck crops. It is slender, usually yellow with light brown areas on the abdominal tergites; in northern areas it may be brown. The most serious thrips pest of many crops is the western flower thrips, *F. occidentalis* (Pergande), which occurs throughout North America, either outdoors or in greenhouses. During colder temperatures or at higher elevations, it is predominantly brown, but in warm temperatures it is yellow with brown areas on the abdominal tergites. In addition to its feeding damage, it is a vector of several tospoviruses causing diseases such as the tomato spotted wilt. During spring in California, this thrips feeds on spider mites on cotton plants. The tobacco thrips, *F. fusca* (Hinds), is also polyphagous and a vector of tomato spotted wilt virus on peanuts in the southern states. It is brown with a light brown fore wing, and is macropterous or brachypterous. The six-spotted thrips, *Scolothrips sexmaculatus* (Pergande), is a little less than a millimeter long and is yellow with three black spots on each front wing. It is predaceous on plant-feeding mites. The grain thrips, *Limothrips cerealium* (Haliday), is a dark brown to black thrips, 1.2 to 1.4 mm long, that feeds on cereals and grasses. It is sometimes quite abundant, forms large flights, and may bite people.

***Family* Phlaeothripidae:** This is the largest family of Thysanoptera, and most species are larger and have a stouter body than the thrips in the suborder Terebrantia. One Australian species, *Idolothrips marginatus* Haliday, is 10–14 mm long. These thrips are mostly dark brown or black, often with light-colored or mottled wings. Most of them feed on fungal mycelia and spores, and breakdown products of fungal action. Some are predaceous, feeding on small insects and mites. A few are plant feeders, and some of these may be of economic importance. The lily bulb thrips, *Liothrips vaneeckei* Priesner, is a dark-colored species about 2 mm long (Figure 23–4C) that feeds on lilies and injures the bulbs. The Cuban laurel thrips, *Gynaikothrips ficorum* (Marchal), feeds on leaves of *Ficus*, a tropical plant grown outdoors and indoors. Feeding by the developing colonies causes curling of the leaves. *Haplothrips leucanthemi* (Schrank) is a black thrips that is common in daisy and red clover flowers. The mullein thrips, *H. verbesci* (Osborn), is often found in European mullein. *Haplothrips kurdjumovi* Karny preys on mite and moth eggs and is found in the eastern and northern states and Canada. The black hunter, *Leptothrips mali* (Fitch), is a fairly common predaceous species. *Aleurodothrips fasciapennis* (Morgan), which is common in Florida, is predaceous on whiteflies.

Collecting and Preserving Thysanoptera

Thrips can be found on flowers, foliage, fruits, bark, and fungi and in debris. The species occurring on vegetation are most easily collected by sweeping. They can be removed from the net by stunning the entire net contents and sorting out the thrips later, or the net contents can be shaken out onto a paper and the thrips picked up with an aspirator or with a moistened camel's-hair brush. Dark species are best seen on a light paper, and light species on a dark paper. If host data are desired, collect the specimens directly from the host plant. The best way to collect flower-frequenting species is to collect the flowers in a paper bag and examine them later in the laboratory. The species that occur in debris and in similar situations are usually collected by means of a Berlese funnel (Figure 35–5) or by sifting the material in which they occur. A beating sheet or its equivalent is very effective for species in all microhabitats.

Thrips should be preserved in liquid and mounted on microscope slides for detailed study. They can be mounted on points, but specimens so mounted are usually not very satisfactory. The best killing solution is AGA, which contains 8 parts of 95% alcohol, 5 parts of distilled water, 1 part of glycerine, and 1 part of glacial acetic acid. After a few weeks, transfer specimens from this solution to 60% ethanol for permanent preservation (Mound and Pitkin 1972). If AGA is not available, 60% ethanol can be used. Avoid significantly higher concentrations, because they harden the body and appendages, creating problems with clearing the specimen and spreading the appendages.

References

Bailey, S. F. 1940. The distribution of injurious thrips in the United States. J. Econ. Entomol. 33(1):133–136.

Bailey, S. F. 1951. The genus *Aeolothrips* Haliday in North America. Hilgardia 21(2):43–80.

Bailey, S. F. 1957. The thrips of California. Part 1: Suborder Terebrantia. Bull. Calif. Insect Surv. 4(5):143–220.

Bailey, S. F., and H. E. Cott. 1954. A review of the genus *Heterothrips* Hood (Thysanoptera: Heterothripidae) in North America, with descriptions of two new species. Ann. Entomol. Soc. Amer. 47:614–635.

Cott, H. E. 1956. Systematics of the Suborder Tubulifera (Thysanoptera) in California. Berkeley: University of California Press, 216 pp.

Heming, B. S. 1991. Order Thysanoptera. In F. W. Stehr (Ed.), Immature Insects, vol. 2, pp. 1–21. Dubuque, IA: Kendall/Hunt.

Heming, B. S. 1993. Structure, function,, ontogeny, and evolution of feeding in thrips (Thysanoptera). In F. C. W. Schaefer and R. A. B. Leschen (Eds.), Functional morphology of insect feeding. Thomas Say Publications in Entomology, Proceedings. Lanham, MD: Entomological Society of America, 162 pp.

Huntsinger, D. M., R. L. Post, and E. U. Balsbaugh, Jr. 1982. North Dakota Terebrantia (Thysanoptera). North Dakota Insects Schafer-Post Series, no. 14. Fargo, ND: Entomology Department, North Dakota State University, 102 pp.

Kirk, W. D. J. 1997. Feeding. In T. Lewis (Ed.), Thrips as Crop Pests. New York: CAB International, 740 pp.

Lewis, T. 1973. Thrips, Their Biology, Ecology and Economic Importance. New York: Academic Press, 350 pp.

Mound, L. A., B. S. Heming, and J. M. Palmer. 1980. Phylogenetic relationships between the families of recent Thysanoptera. Zool. J. Linn. Soc. London 69:111–141.

Mound, L. A., and R. Marullo. 1996. The thrips of Central and South America: an introduction (Insecta: Thysanoptera). Mem. Entomol. Internat. 6:1–487.

Mound, L. A., and R. Marullo. 1998. Two new basal-clade Thysanoptera from California with Old World affinities. J. New York Entomol. Soc. 106:81–94.

Mound, L. A., and K. O'Neill. 1974. Taxonomy of the Merothripidae, with ecological and phylogenetic considerations (Thysanoptera). J. Nat. Hist. 8:481–509.

Mound, L. A., and B. R. Pitkin. 1972. Microscopic wholemounts of thrips (Thysanoptera). Entomol. Gaz. 23:121–125.

Nakahara, S. 1994. The genus *Thrips* Linnaeus (Thysanoptera: Thripidae) of the New World. USDA Tech. Bull. 1822:1–183.

Nakahara, S. 1995. Review of the Nearctic species of *Anaphothrips* (Thysanoptera: Thripidae). Insecta Mundi 9:221–248.

Nakahara, S. 1995. *Ewartithrips*, new genus (Thysanoptera: Thripidae) and four new species from California. J. New York Entomol. Soc. 103:229–250.

O'Neill, K., and R. S. Bigelow. 1964. The *Taeniothrips* of Canada. Can. Entomol. 96:1219–1239.

Pesson, P. 1951. Ordre des Thysanoptera Haliday, 1836 (= Physapoda Burm., 1838) ou thrips. Traité de Zoologie 10:1805–1869.

Peterson, A. 1915. Morphological studies on the head and mouthparts of the Thysanoptera. Ann. Entomol. Soc. Amer. 8:20–67.

Sakimura, K., and K. O'Neill. 1979. *Frankliniella*, redefinition of genus and revision of *minuta* group species (Thysanoptera: Thripidae). USDA Tech. Bull. 1572. 49 pp.

Stannard, L. J. 1957. The phylogeny and classification of the North American genera of the suborder Tubulifera (Thysanoptera). Ill. Biol. Monogr. No. 25, 200 pp.

Stannard, L. J. 1968. The thrips, or Thysanoptera, of Illinois. Bull. Ill. Nat. Hist. Surv. 29:215–552.

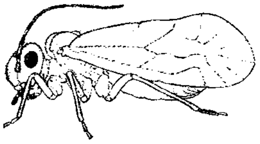
Thomasson, G. L., and R. L. Post. 1966. North Dakota Tubulifera (Thysanoptera). North Dakota Insects Publ. No. 6. Fargo, ND: Department of Entomology, Agricultural Experiment Station, North Dakota State University, 58 pp.

Vance, T. C. 1974. Larvae of Sericothripini (Thysanoptera: Thripidae), with reference to other larvae of the Terebrantia of Illinois. Bull. Ill. Nat. Hist. Surv. 31:143–208.

Wilson, T. H. 1975. A monograph of the subfamily Panchaetothripinae (Thysanoptera: Thripidae). Mem. Amer. Entomol. Inst. 23:1–354.

24

Order Psocoptera[1,2]
Psocids



The psocids are small, soft-bodied insects, most of which are less than 6 mm long. Wings may be present or absent, and both long-winged and short-winged individuals occur in some species. The winged forms have four membranous wings (rarely two, with the hind wings vestigial). The fore wings are a little larger than the hind wings, and the wings at rest are usually held rooflike over the abdomen. The antennae are generally fairly long; the tarsi are two- or three-segmented; and cerci are lacking. Psocids have mandibulate mouthparts, and the clypeus is large and somewhat swollen. The metamorphosis is simple (Figure 24–1).

Some 85 genera and about 340 species of psocids are known from the United States and Canada, but most people see only a few species that live in houses or other buildings. Most species found in buildings are wingless and, because they often live among books or papers, are usually called *booklice*. The majority of the psocids are outdoor species with well-developed wings. They live on the bark or foliage of trees and shrubs, under bark or stones, or in dead leaves. These psocids are sometimes called *barklice*.

Some psocids feed on algae and lichens. Others feed on molds, cereals, pollen, fragments of dead insects, and similar materials. The term "lice" in the names "booklice" and "barklice" is somewhat misleading, because none of these insects is parasitic, although a few are phoretic on birds and mammals. Relatively few are louselike in appearance. The species living in buildings rarely cause much damage, but are frequently a nuisance.

The eggs of psocids are laid singly or in clusters and are sometimes covered with silk or debris. Most species pass through six nymphal instars. Some species are gregarious, living under thin silk webs. One southern species, *Archipsocus nomas* Gurney, often makes rather conspicuous webs on tree trunks and branches.

Certain psocids (species of *Liposcelis* and *Rhyopsocus*) have been found capable of acting as intermediate hosts of the fringed tapeworm of sheep, *Thysanosoma ostinioides* Diesing.

Classification of the Psocoptera

A number of different classifications have been used for Psocoptera, and they differ in the principal criteria used in dividing up the order, the number of families recognized, and the placement of some genera. The principal classifications are those of Pearman (1936), Roesler (1944), Badonnel (1951), and Smithers (1972). We follow here the arrangement of Badonnel, with minor revisions.

A synopsis of the Psocoptera in the United States and Canada is given next, with alternate names and arrangements in parentheses. The groups marked with an asterisk (*) are seldom encountered.

Suborder Trogiomorpha
    Lepidopsocidae
    Trogiidae (Atropidae)
    Psoquillidae (Trogiidae in part)
    Psyllipsocidae (Psocatropidae)
    Prionoglarididae (Psyllipsocidae, in part)*

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[1] Psocoptera: *psoco*: rub small; *ptera*, wings (referring to the gnawing habits of these insects).

[2] This chapter was prepared by Edward L. Mockford.

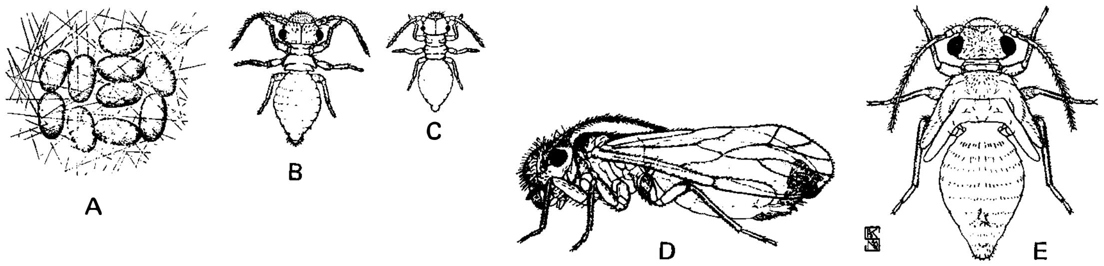


Figure 24–1 Developmental stages of the psocid *Ectopsocopsis cryptomeriae* (Enderlein) (Ectopsocidae). A, eggs; B, third instar; C, first instar; D, adult female; E, sixth instar. (Courtesy of Sommerman.)

Suborder Troctomorpha
- Liposcelididae
- Pachytroctidae
- Sphaeropsocidae (Pachytroctidae in part)*
- Amphientomidae

Suborder Psocomorpha (Eupsocida)
- Epipsocidae
- Ptiloneuridae (Epipsocidae in part)*
- Caeciliusidae (Caeciliidae, Polypsocidae)
- Stenopsocidae (Caeciliusidae)
- Amphipsocidae (Stenopsocidae, Polypsocidae)
- Dasydemellidae (Amphipsocidae)
- Asiopsocidae (Caeciliusidae)*
- Elipsocidae (Pseudocaeciliidae in part)
- Philotarsidae (Pseudocaeciliidae in part)
- Mesopsocidae (Pseudocaeciliidae in part)
- Lachesillidae (Pseudocaeciliidae in part)
- Peripsocidae (Pseudocaeciliidae in part)
- Ectopsocidae (Pseudocaeciliidae in part, Peripsocidae in part)
- Pseudocaeciliidae
- Trichopsocidae (Pseudocaeciliidae in part)
- Archipsocidae (Pseudocaeciliidae in part)
- Hemipsocidae (Pseudocaeciliidae in part)*
- Myopsocidae
- Psocidae

Key to the Families of Psocoptera

The families marked with an asterisk (*) are small and are unlikely to be encountered by the general collector. This key is based on adults (for a key to nymphs, see Mockford 1987). All psocid nymphs have two-segmented tarsi, either no wing pads or fleshy wing pads (Figure 24–1E), and no external genitalia (Figure 24–2F). It is necessary to make at least temporary slide preparations for some parts of this key; see the section on collecting and preserving Psocoptera, at the end of the chapter.

1. Antennae with more than 20 segments; segments never secondarily annulated; tarsi 3-segmented (suborder Trogiomorpha) 2

1′. Antennae with 17 or fewer segments; if more than 13 segments present, some or all flagellar segments secondarily annulated (Figure 24–3A); tarsi 2- or 3-segmented 6

2(1). Female with ovipositor valvulae of opposite sides separated by a space or touching only at or near their apices (Figure 24–2A); subgenital plate not much reduced (Figure 24–2A); in long-winged forms, veins Cu$_2$ and 1A of fore wing ending together or very close on wing margin (Figure 24–4B); hind wings with one closed cell; wings never clothed in scales or dense hairs; venation persistent in short-winged forms 3

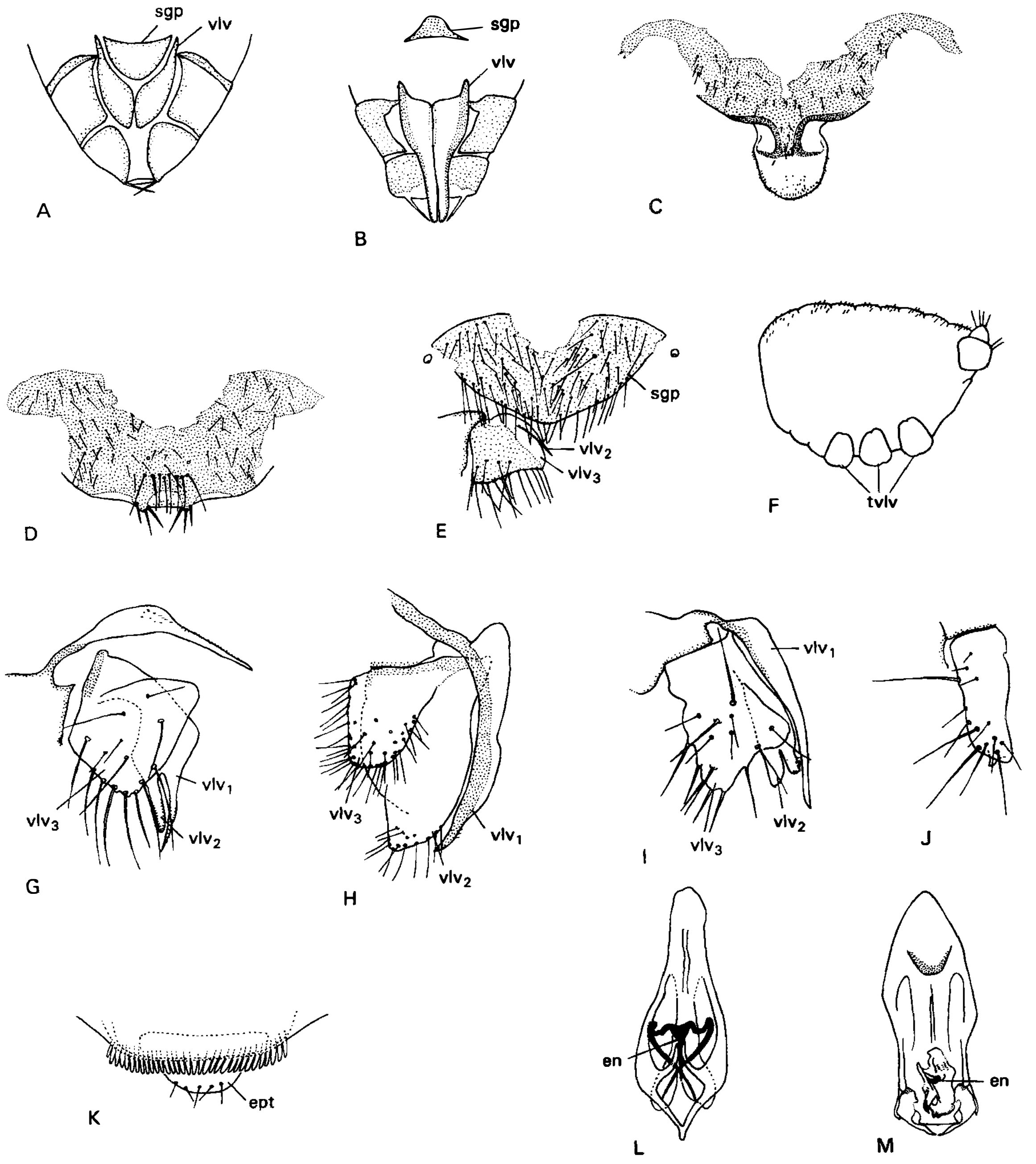


Figure 24–2 Abdominal structures of Psocoptera. A, *Psyllipsocus*, female (Psyllipsocidae), terminal abdominal segments, ventral view; B, *Echmepteryx*, female (Lepidopsocidae), terminal abdominal segments, ventral view; C, subgenital plate of female *Mesopsocus* (Mesopsocidae); D, subgenital plate of female *Elipsocus* (Elipsocidae); E, subgenital plate and left ovipositor valvulae of *Archipsocus* (Archipsocidae); F, lateral view of abdomen of nymph of Amphipsocidae; G, ovipositor valvulae of *Trichopsocus* (Trichopsocidae); H, ovipositor valvulae of *Peripsocus* (Peripsocidae); I, ovipositor valvulae of *Nepiomorpha* (Elipsocidae); J, left ovipositor valvulae of *Lachesilla* (Lachesillidae); K, comb of 10th abdominal tergum of *Ectopsocus* male (Ectopsocidae); L, phallosome of *Peripsocus* male (Peripsocidae); M, phallosome of *Ectopsocus* male (Ectopsocidae). *en*, endophallus; *ept*, epiproct; *sgp*, subgenital plate; *tv*, transverse vesicle; vlv_{1-3}, ovipositor valvulae 1–3.

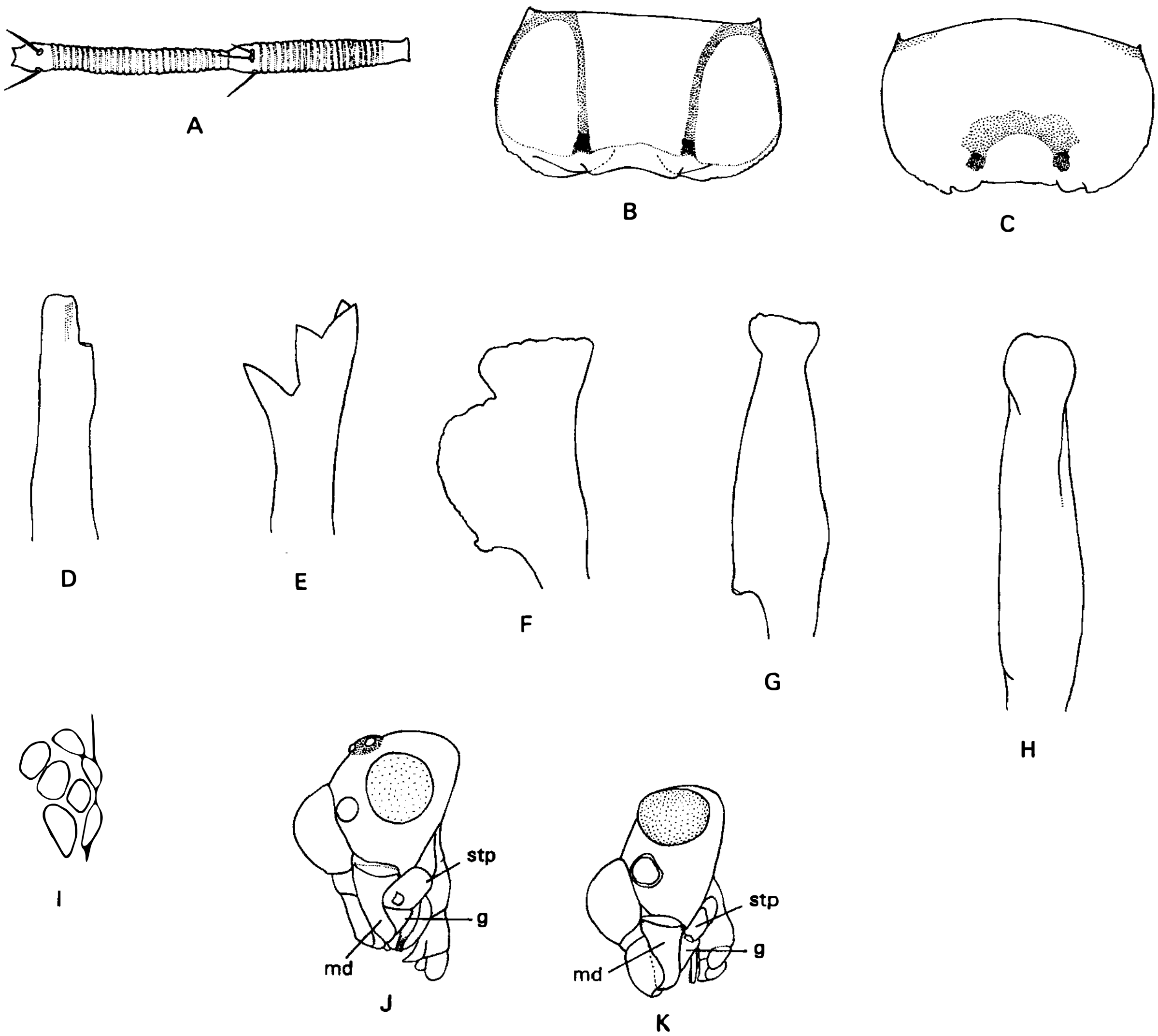


Figure 24–3 Head structures of Psocoptera. A, flagellar segments 1 and 2 of *Liposcelis* (Liposcelididae); B, labrum of *Loneura* (Ptiloneuridae); C, labrum of *Indiopsocus* (Psocidae); D, distal end of lacinia of *Speleketor* (Prionoglarididae); E, distal end of lacinia of *Psyllipsocus* (Psyllipsocidae); F, distal end of lacinia of *Asiopsocus* (Asiopsocidae); G, distal end of lacinia of *Teliapsocus* (Dasydemellidae); H, distal end of lacinia of *Valenzuela* (Caeciliusidae); I, ocular elements of *Liposcelis* (Liposcelididae); J, lateral view of head of *Teliapsocus*; K, lateral view of head of *Mesopsocus* (Mesopsocidae). *g*, galea; *md*, mandible; *stp*, stipes.

2′. Female with ovipositor valvulae of opposite sides touching along ventral midline (Figure 24–2B); subgenital plate much reduced; in long-winged forms, veins Cu_2 and 1A of fore wing ending separately on wing margin (Figure 24–4C); hind wing with no closed cells, or if 1 closed cell present then at least fore wing densely clothed with scales or hairs (Figure 24–4D); wings reduced in some forms (venation absent in some of these) 4

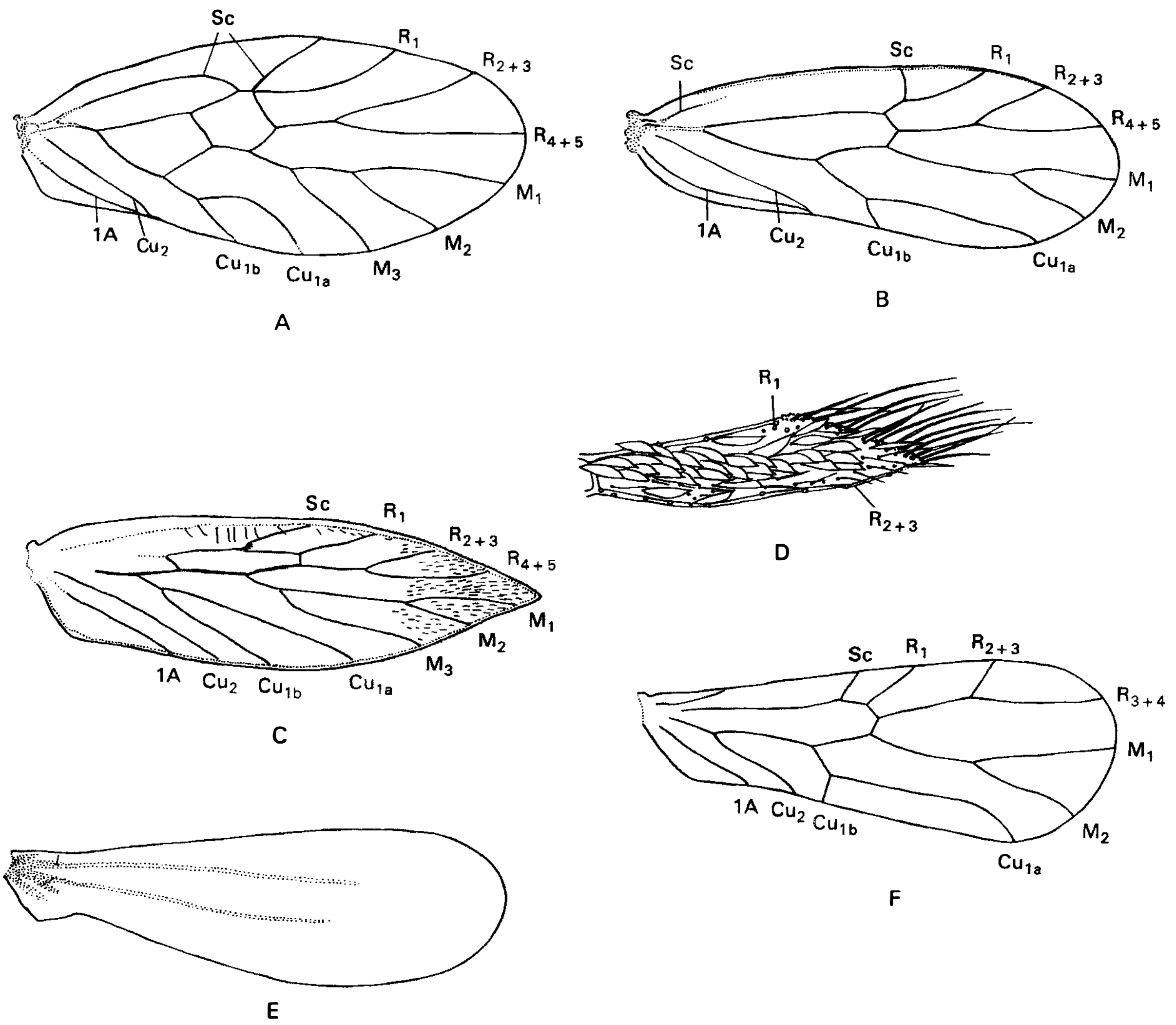


Figure 24–4

Front wings of Trogiomorpha and Troctomorpha. A, *Speleketor* (Prionoglarididae); B, *Psyllipsocus* (Psyllipsocidae); C, *Echmepteryx*, scales and marginal hairs removed (Lepidopsocidae); D, *Echmepteryx*, cell R_1, enlarged, scales and marginal hairs intact; E, *Embidopsocus* (Liposcelididae); F, *Nanopsocus* (Pachytroctidae).

3(2).	Sc of fore wing describing a curve and rejoining R_1 distally (Figure 24–4A); lacinia totally absent or at least lacking terminal tines (Figure 24–3D)	Prionoglarididae*	p. 351
3′.	Segment of Sc in fore wing absent from near wing base to base of pterostigma (Figure 24–4B); lacinia persistent in adult and with terminal tines (Figure 24–3E)	Psyllipsocidae	p. 351
4(2′).	Body and fore wings densely clothed in scales or long hairs or both (Figure 24–4D); fore wings usually well developed, usually pointed apically (Figure 24–4C), never reduced to pads extending less than one fourth length of abdomen	Lepidopsocidae	p. 351

4′.	Body and wings never scaled; fore wings variably developed, from fully developed to nearly absent	5	
5(4′).	Fore wings well developed or reduced, but always with veins (Figure 24–5C); hind wings developed or absent	Psoquillidae	p. 351
5′.	Fore wings reduced to tiny scales or buttons (Figure 24–5B), never with veins	Trogiidae	p. 351
6(1′).	Antennae 11- to 17-segmented, with secondary annulations (Figure 24–3A) (suborder Troctomorpha)	7	
6′.	Antennae 13-segmented, lacking secondary annulations (suborder Psocomorpha)	10	

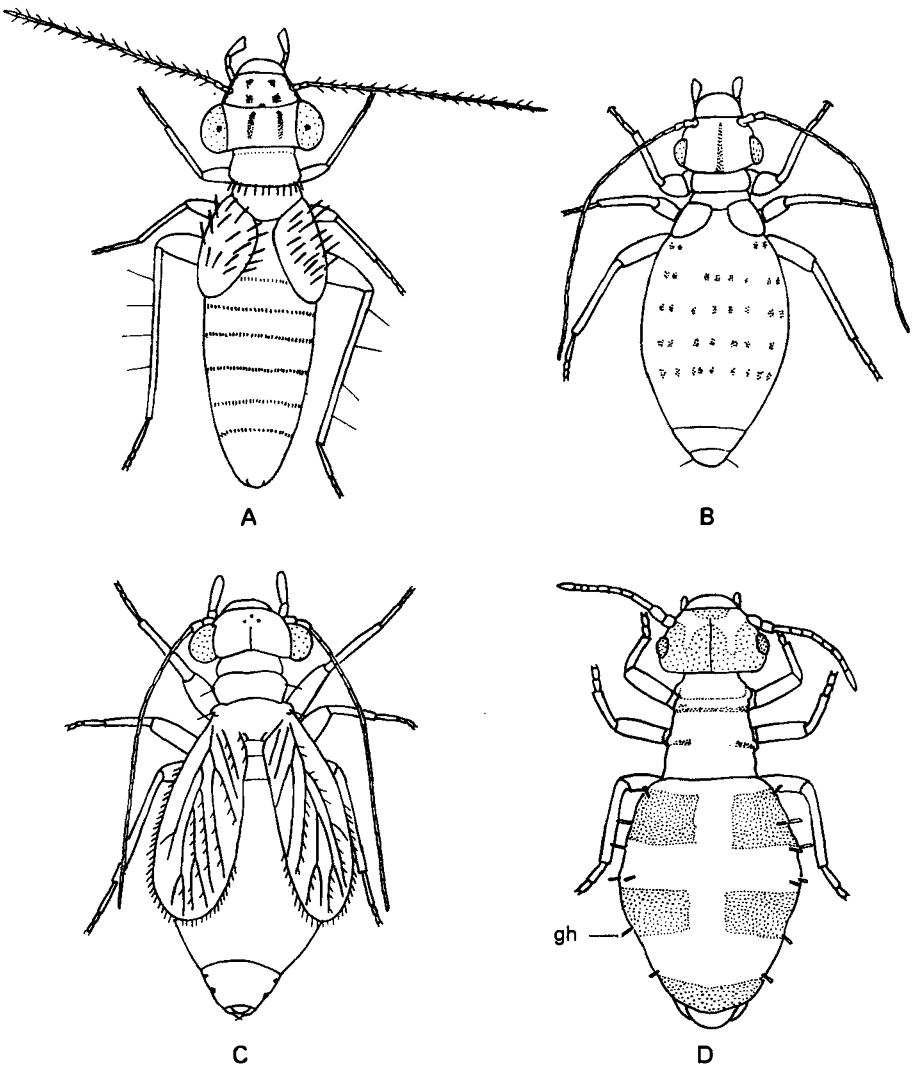


Figure 24–5 Short-winged Psocoptera. A, *Neolepolepis occidentalis* (Mockford) (Lepidopsocidae); B, *Trogium pulsatorium* (L.) (Trogiidae); C, *Rhyopsocus bentonae* Sommerman (Psoquillidae); D, *Nepiomorpha perpsocoides* Mockford (Elipsocidae). *gh*, gland hair.

7(6).	Wings, when present, never scaled; either held flat over back when at rest with fore wing of one side largely covering that of other side, or fore wings elytriform; wings frequently reduced or absent	8	
7′.	Wings always present, not held flat over back in repose; fore wings clothed with scales, never elytriform	Amphientomidae	p. 353
8(7).	Fore wings, when present, with complete venation (Figure 24–4F); mesothorax and metathorax distinctly separate in both winged and wingless forms	Pachytroctidae	p. 352
8′.	Fore wings, when present, with venation greatly reduced (Figure 24–4E); in all apterous forms mesothorax and metathorax indistinguishably fused	9	
9(8′).	In alate forms, both front and hind wings present, flat and delicate; eyes near vertex, hemispherical, compound; in apterous forms, eyes removed from vertex, each consisting of 2 large elements alone or preceded by 8 or fewer smaller ocelloids (Figure 24–3I); thoracic sterna broad and bearing setae (Figure 24–6A)	Liposcelididae	p. 351
9′.	In alate forms, fore wings convex, elytriform; in all forms, eyes removed from vertex, composed of few ocelloids, none greatly enlarged; thoracic sterna narrow, without setae	Sphaeropsocidae*	p. 353
10(6′).	Head long dorsoventrally; labrum with 2 oblique, strongly sclerotized ridges internally that are clearly visible externally (Figure 24–3B); wings usually much reduced; long-winged forms with Rs and M of fore wing not touching, connected by distinct crossvein (Figure 24–7A,B)	11	
10′.	Head short, wide; labrum internally on either side with only small sclerotized tubercle, the two sometimes connected by sclerotized arch; below arch, or between the pair of tubercles lies a clear semicircular area bordering anterior margin (Figure 24–3C); long-winged forms with Rs and M of fore wing variable, joined together for short distance, or at a point, or by crossvein	12	

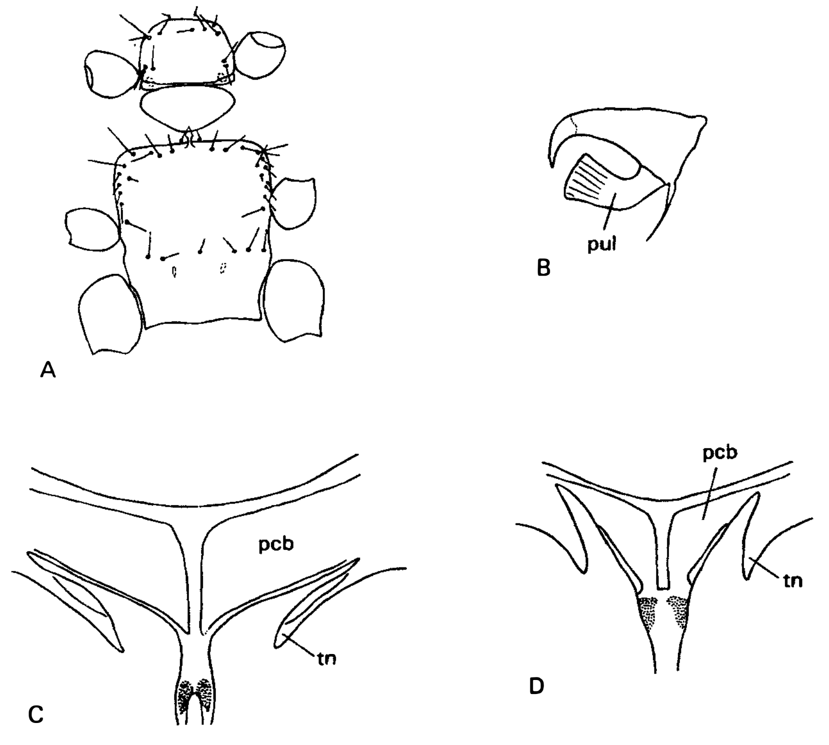


Figure 24–6 Thoracic structures of Psocoptera. A, thoracic sterna and leg bases of *Embidopsocus* (Liposcelididae); B, tarsal claw of *Teliapsocus* (Amphipsocidae); C, mesosternum of *Mesopsocus* (Mesopsocidae); D, mesosternum of *Trichadenotecnum* (Psocidae). *pul*, pulvillus; *pcb*, precoxal bridge; *tn*, trochantin.

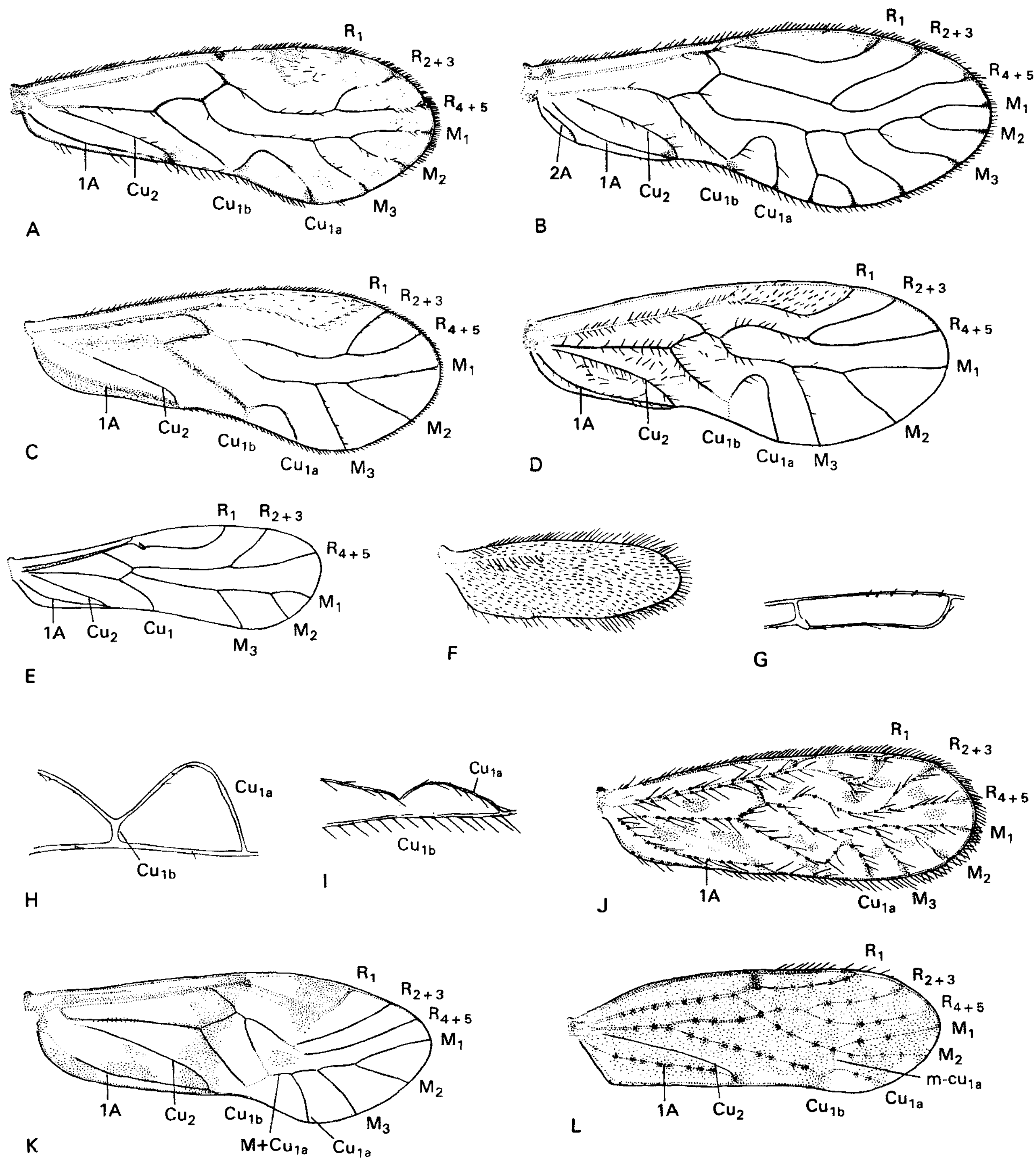


Figure 24–7 Front wings of Psocomorpha. A, *Epipsocus* (Epipsocidae); B, *Loneura* (Ptiloneuridae); C, *Valenzuela* (Caeciliusidae); D, *Teliapsocus* (Dasydemellidae); E, *Palmicola*, male (Elipsocidae); F, *Archipsocus*, female (Archipsocidae); G, pterostigma of *Ectopsocus* (Ectopsocidae); H, cell Cu_{1a} of *Lachesilla* (Lachesillidae); I, cell Cu_{1a} of *Trichopsocus* (Trichopsocidae); J, *Aaroniella* (Philotarsidae); K, *Indiopsocus* (Psocidae); L, *Hemipsocus* (Hemipsocidae).

11(10).	Fore wing with 1 anal vein (Figure 24–7A) or wings greatly reduced; tarsi 2-segmented	Epipsocidae	p. 353
11′.	Fore wings never reduced, with 2 anal veins (Figure 24–7B); tarsi 3-segmented	Ptiloneuridae*	p. 353
12(10′).	Mandibles at least somewhat elongate, usually concave posteriorly (Figure 24–3J), the concavity filled by bulging stipes and galea; labrum broad; preapical denticle never present on tarsal claws (Figure 24–6B)	13	
12′.	Mandibles short, not decidedly concave posteriorly (Figure 24–3K), stipes and galea relatively flat; labrum rounded, closely adhering to contour of mandibles; preapical denticle present or absent on tarsal claws	17	
13(12).	Abdomen ventrally with 2 or 3 transverse vesicles capable of being inflated (Figure 24–2F); lacinial tip variable but not extremely broad (Figure 24–3G,H)	14	
13′.	Abdomen ventrally lacking transverse vesicles, lacinial tip very broad (Figure 24–3F) (*Asiopsocus*)	Asiopsocidae*	p. 353
14(13).	Setae of fore wing veins relatively short, slanting distally, mostly single-ranked (Figure 24–7C); pterostigma-rs crossvein present or not in fore wing	15	
14′.	Setae of fore wing veins relatively long, upright, mostly in more than one rank (Figure 24–7D), pterostigma-rs crossvein absent	16	
15(14).	Pterostigma-rs crossvein and m-cu$_{1a}$ crossvein present in fore wing; hind wing with marginal setae restricted to cell R3	Stenopsocidae	p. 353
15′.	Pterostigma-rs and m-cu$_{1a}$ crossveins absent; hind wing with marginal setae around most of wing	Caeciliusidae	p. 353
16(14′).	Ciliation of hind wing margin restricted to cell R3, sparse; M in fore wing 3-branched	Dasydemellidae	p. 353
16′.	Ciliation continuous around most of margin of hind wing; M in fore wing 2-branched (*Polypsocus*)	Amphipsocidae	p. 353
17(12′).	Wings fully developed or only slightly reduced	18	
17′.	Wings greatly reduced; venational characters not usable	32	
18(17).	Mesothoracic precoxal bridges narrow at point of junction with trochantin (Figure 24–6D), trochantin broad basally, tapering distally	19	
18′.	Mesothoracic precoxal bridges wide at point of junction with trochantin (Figure 24–6C), trochantin narrow throughout	21	
19(18).	Tarsi 2-segmented	20	
19′.	Tarsi 3-segmented	Myopsocidae	p. 354
20(19).	Cu$_{1a}$ of fore wing joined directly to M; M in fore wing 3-branched (Figure 24–7K)	Psocidae	p. 354
20′.	Cu$_{1a}$ in fore wing joined to M by a crossvein; M in fore wing 2-branched (Figure 24–7L)	Hemipsocidae*	p. 354
21(18′).	Margin of fore wing with "crossing hairs" between veins R$_{4+5}$ and Cu$_{1a}$ (Figure 24–7J)	22	
21′.	Margin of fore wing without "crossing hairs"	24	
22(21).	Tarsi 3-segmented	Philotarsidae	p. 353
22′.	Tarsi 2-segmented	23	
23(22′).	Surface of fore wing densely hairy, venation of fore wing obscure (Figure 24–7F); forms living in colonies under dense webs	Archipsocidae	p. 354
23′.	Surface of fore wing with hairs largely confined to veins and margin; venation of both wings distinct; solitary forms living freely or under sparse webbing	Pseudocaeciliidae	p. 354

24(21′).	Tarsi 3-segmented	25	
24′.	Tarsi 2-segmented	26	
25(24).	Wings bare; subgenital plate with single central, posteriorly directed lobe (Figure 24–2C)	Mesopsocidae	p. 354
25′.	Wings with obvious hairs on veins and margins; subgenital plate never with central, posteriorly directed lobe, usually with 2 lobes (Figure 24–2D)	Elipsocidae	p. 353
26(24′).	Vein Cu$_1$ in fore wing branched (Cu$_{1a}$ present)	27	
26′.	Vein Cu$_1$ in fore wing simple (Cu$_{1a}$ absent)	29	
27(26).	Cubital loop in fore wing low (Figure 24–7I); numerous setae on veins and margins of wings; females with 3 complete pairs of ovipositor valvulae (Figure 24–2G)	28	
27′.	Cubital loop in fore wing higher (Figure 24–7H) or joined to M; setae sparse or absent on veins and margins of wings; ovipositor valvulae reduced to a single valvula on each side (Figure 24–2J)	Lachesillidae	p. 353
28(27).	Pale, delicate forms found on foliage	Trichopsocidae	p. 354
28′.	Darker-bodied forms found on tree trunks and stone outcrops (males of *Reuterella*)	Elipsocidae	p. 353
29(26′).	Pterostigma constricted basally (as in Figure 24–7A–E,J,K); if M of fore wing 3-branched, setae sparse or absent on veins and margin of wing; if M of fore wing 2-branched, setae abundant on veins and wing margin	30	
29′.	Pterostigma not constricted basally (Figure 24–7G); M of fore wing 3-branched	Ectopsocidae	p. 354
30(29).	M in fore wing 2-branched; setae abundant on veins and margin of fore wing (*Notiopsocus*)	Asiopsocidae*	p. 353
30′.	M in fore wing 3-branched; setae sparse or absent on veins and margin of fore wing	31	
31(30′).	Free-living forms (females) with body with numerous "gland hairs," that is, hairs widest apically; solitary forms (males) living under dense webbing; third valvula of ovipositor large, covering most of second in normal position (Figure 24–2I) (*Nepiomorpha* and *Palmicola*)	Elipsocidae	p. 353
31′.	Body without "gland hairs," forms not living under webs; third valvula of ovipositor much smaller than second (Figure 24–2H)	Peripsocidae	p. 353
32(17′).	Tarsi 3-segmented; only females, all with single central posterior projection on subgenital plate (Figure 24–2C); large, robust forms with wings reduced to tiny knobs, length 4–5 mm	Mesopsocidae	p. 353
32′.	Tarsi 2-segmented; smaller forms, including males	33	
33(32′).	Males and females both bearing a conspicuous white, crosslike mark dorsally on abdomen (Figure 24–5D) and body with numerous gland hairs (Figure 24–5D, see couplet 29) (*Nepiomorpha*)	Elipsocidae	p. 353
33′.	Body not marked as in preceding entry; gland hairs, if present, very restricted in distribution	34	
34(33′).	Females with 2 pairs of ovipositor valvulae (Figure 24–2E) or none; subgenital plate evenly rounded on its posterior margin (Figure 24–2E); males never with transverse comb on posterior margin of abdominal tergum 10; subtropical and tropical forms living under dense webs	Archipsocidae	p. 354
34′.	Females with either 1 pair or 3 pairs of ovipositor valvulae; posterior margin of subgenital plate variously developed; males with transverse comb on posterior margin of abdominal tergum 10; either free-living forms, forms living in small groups under scanty webbing, or forms living solitarily under dense webbing	35	

35(34′).	Females, with either 1 or 3 pairs of ovipositor valvulae	36	
35′.	Males, with phallosome (Figure 24–2L,M) visible through cuticle of ninth abdominal sternum	40	
36(35).	Ovipositor reduced to single, thumblike valvula on each side (Figure 24–2J)	Lachesillidae	p. 353
36′.	Ovipositor with 3 pairs of valvulae	37	
37(36′).	Relatively large forms, over 3 mm long; third ovipositor valvula never greatly reduced; subgenital plate with single central lobe (*Camelopsocus* and *Blaste*)	Psocidae	p. 354
37′.	Smaller forms, less than 3 mm long; third ovipositor valvula sometimes reduced (Figure 24–2H); subgenital plate variously developed	38	
38(37′).	Fore winglets relatively large, at least one third length of abdomen; third ovipositor valvula reduced (Figure 24–2H)	Peripsocidae	p. 353
38′.	Fore winglets much smaller or absent; third ovipositor valvula not reduced	39	
39(38′).	Winglets obvious, decidedly protruding from thoracic surface; vertex of head with some conspicuous setae longer than antennal pedicel	Ectopsocidae	p. 354
39′.	Winglets reduced to slight swellings on thoracic surface; vertex of head with only very short setae, none as long as antennal pedicel; forms living solitarily under dense webbing	Elipsocidae	p. 353
40(35′).	Vertex bearing distinct setae; phallosome with asymmetrical endophallus (Figure 24–2M)	Ectopsocidae	p. 354
40′.	Vertex with only minute setae or none; phallosome with symmetrical endophallus (Figure 24–2L)	Peripsocidae	p. 353

Suborder Trogiomorpha

The members of suborder Trogiomorpha have more than 20 antennal segments, the labial palps are two-segmented, and the tarsi are three-segmented. Antennal flagellar segments are never secondarily annulated, although rings of microtrichia that resemble annulations are sometimes present.

Family **Lepidopsocidae:** These psocids live on trees, shrubs, and stone outcrops. The wings are slender, usually pointed apically, and wings and body are usually covered with scales. The group is primarily tropical, with 15 species in the United States. *Echmepteryx hageni* (Packard) is common on trees and stone outcrops throughout the eastern states.

Family Trogiidae: Most members of this family have the wings reduced, but none are completely wingless. Species of *Cerobasis* are common on shrubs and trees in the Southwest. A few species live in buildings: *Lepinotus inquilinus* Heyden is often found in granaries, and *Trogium pulsatorium* (L.) lives in houses, barns, and granaries in the Northeast. Females of some trogiids produce a sound by tapping the abdomen on the substrate.

Family **Psoquillidae:** Members of this family may be fully winged or have the wings in various stages of reduction, but always with distinct venation. *Psoquilla marginepunctata* Hagen lives in houses in the Southeast. Species of *Rhyopsocus* live in dead leaves hanging on plants and in ground litter in the southern states.

Family **Psyllipsocidae:** The psyllipsocids are pale-colored and live in a variety of situations. *Psyllipsocus ramburii* Selys-Longchamps lives in damp, dark places such as cellars and caves. It is common around the openings of wine and vinegar barrels. *Psyllipsocus oculatus* Gurney lives on persistent dead leaves of yucca plants in arid areas of the Southwest. Both long- and short-winged individuals occur in most species.

Family **Prionoglarididae:** This family is represented in the United States by the genus *Speleketor*, medium-sized, rather pale forms with broad, unmarked wings. They live in caves and on the skirts of the native palm *Washingtonia filifera* in the Southwest.

SUBORDER **Troctomorpha:** The members of this suborder have more than 13 but fewer than 20 antennal segments, with the flagellar segments secondarily annulated (Figure 24–3A). The labial palpi are two-segmented, and the tarsi are three-segmented.

Family **Liposcelididae:** Most members of this group live under bark, in dead leaves and dead grass, and in bird and mammal nests. They are either fully winged with wings held flat over the back at rest, or completely wingless. Several species of *Liposcelis* live commonly in buildings. They are found in dusty places where the temperature and humidity are high, on shelves, in cracks of windowsills, behind loose wallpaper, and in similar situations. They are wingless psocids about 1 mm long, with enlarged hind femora (Figure 24–8D). *Liposcelis bostrychophila* Badonnel has become a rather important pest in houses and warehouses in Europe, Australia, and parts of North America.

Family **Pachytroctidae:** Only six species in this family occur in the United States. *Nanopsocus oceanicus* Pearman lives in houses in the Southeast. It and several

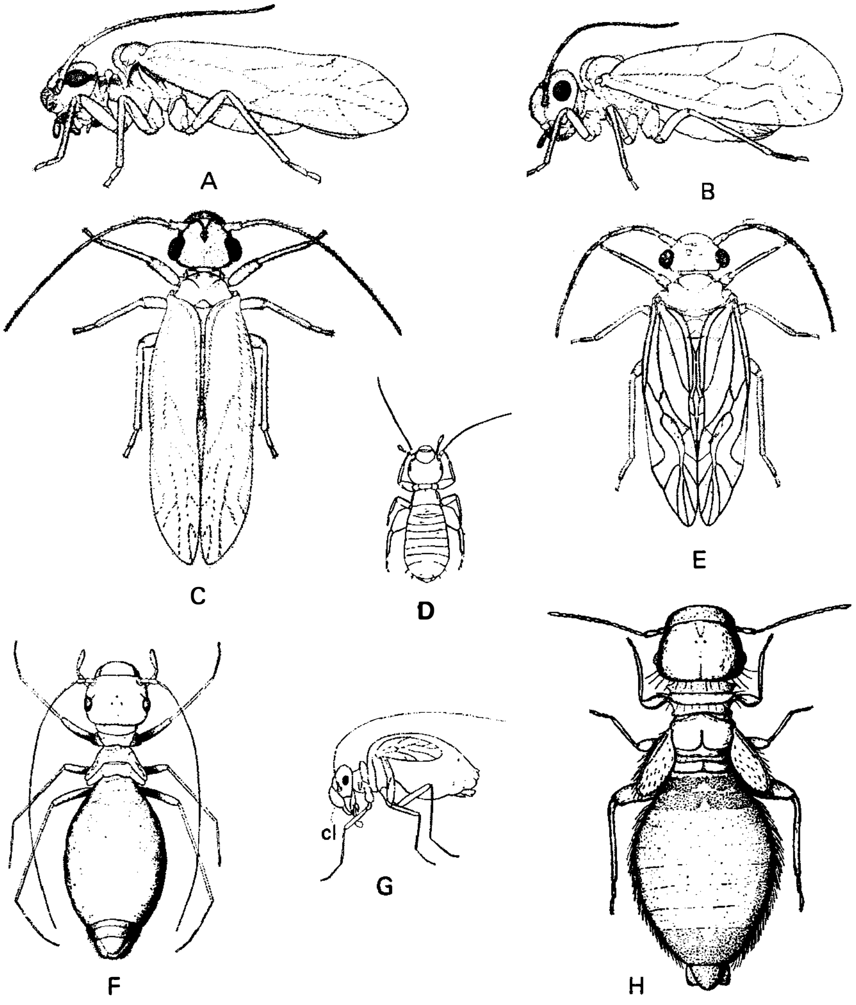


Figure 24–8 Psocids. A, *Valenzuela manteri* (Sommerman), female, lateral view (Caeciliusidae); B, *Anomopsocus amabilis* (Walsh), female, lateral view (Lachesillidae); C, *Valenzuela manteri*, female, dorsal view; D, *Liposcelis* sp., dorsal view (Liposcelididae); E, *Anomopsocus amabilis*, female, dorsal view; F, *Psyllipsocus ramburii* Selys, short-winged female, dorsal view (Psyllipsocidae); G, *Psocathropos* sp., lateral view (Psyllipsocidae), *cl*, clypeus; H, *Archipsocus nomas* Gurney, short-winged female, dorsal view (Archipsocidae). (A–C, E, courtesy of Sommerman; F, courtesy of Gurney; D and G reprinted by permission of Pest Control Technology, National Pest Control Association; A, E, courtesy of the Entomological Society of Washington; B, E, F, courtesy of the Entomological Society of America; H, courtesy of the Washington Academy of Science.)

species of *Tapinella* live on leaves of native palms in the Gulf states.

Family **Sphaeropsocidae:** These are small psocids with elytriform fore wings. Two species have been found in ground litter in California.

Family **Amphientomidae:** These psocids resemble the Lepidopsocidae in having the wings and body covered with scales. They are mainly tropical, but one species of *Stimulopalpus*, *S. japonicus* Enderlein, has been introduced from Asia and lives commonly on cement structures and stone outcrops in forest areas from Virginia and North Carolina west to Arkansas.

SUBORDER **Psocomorpha:** The antennae in these psocids usually have 13 segments, never more. The labial palps are one-segmented, and the tarsi are two- or three-segmented.

Family **Epipsocidae:** This family is represented in the United States by four species. Two species of *Bertkauia* are moderately common, one on shaded rock outcrops and adjacent tree trunks, the other in forest ground litter. Two species of *Epipsocus*, probably introduced from the American tropics, occur in southern Florida.

Family **Ptiloneuridae:** This Neotropical group is closely related to the Epipsocidae. It is represented in the United States by a single, rare species occurring on stone outcrops in southern Arizona.

Family **Caeciliusidae:** These are leaf-inhabiting psocids on both conifers and broad-leaf trees. Most are long-winged, but some ground litter species have both long-winged and short-winged females. Five genera are known in the United States, with 33 species.

Family **Stenopsocidae:** These are leaf-inhabiting psocids similar to the caeciliusids, but with the two crossveins mentioned in the key and with setae on the hind wing margin restricted to cell R3. The single species in the United States, *Graphopsocus cruciatus* (L.), is common in the southeastern states and on the Pacific Coast from California north to Washington. It was probably introduced from Europe.

Family **Amphipsocidae:** These psocids resemble the caeciliusids, but are larger with relatively longer hairs on wings and antennae. They are also leaf inhabitants. Only one species, *Polypsocus corruptus* Hagen is known in the United States.

Family **Dasydemellidae:** Like the Amphipsocidae, these are relatively large psocids. Wing setae are sparser, and those of the hind wing are restricted to the margin in cell R3. These psocids are found on woody stems and dead hanging leaves. The single native species, *Teliapsocus conterminus* (Walsh), is found on both coasts, inland to the mountains in both East and West, around the Great Lakes, and up the Mississippi Embayment to southern Missouri. A second species, *Dasydemella sylvestrii* Enderlein, native to Mexico, was taken at a port of entry in Texas.

Family **Asiopsocidae:** These psocids appear to be inhabitants of twigs of small trees and shrubs. One species of *Asiopsocus*, *A. sonorensis* Mockford and Garcia-Aldrete, occurs in southern Arizona. The tropical genera *Notiopsocus* and *Pronotipsocus* each have a representative in southern Florida.

Family **Elipsocidae:** This family includes forms with 2- as well as 3-segmented tarsi. Fifteen species in six genera are known from the United States. *Cuneopalpus cyanops* (Rostock) was introduced from Europe and has become established in coastal regions of California and New York. Four species of *Elipsocus*, probably introduced from Europe, live on conifers and broad-leaf trees in the Pacific Northwest. Native species of this genus, some still undescribed, are found in the Rocky Mountains and other upland areas, as well as in conifer forests in northern Wisconsin. *Propsocus pulchripenis* (Perkins), of unknown origin, is established in some coastal counties of California. *Reuterella helvimacula* Enderlein, also known from Europe, lives on stone outcrops and tree trunks in several northern states. Species of *Palmicola* live on palms, oaks, and conifers in the southeastern states.

Family **Philotarsidae:** This is one of several families in which setae of the posterodistal margin of the fore wing form a series of crossing pairs (Figure 24–7J). North American species have three tarsal segments. Although only six species are known from the United States, these insects may become abundant locally in late summer. *Philotarsus kwakiutl* Mockford is common on conifers in the Pacific Northwest; *Aaroniella badonnedi* (Danks) is often abundant on trunks and branches of trees and on stone outcrops in the southern part of the Midwest.

Family **Mesopsocidae:** These are relatively large psocids found on branches of coniferous and broad-leaf trees. Only three species of this primarily Old World family occur in the United States. *Mesopsocus unipunctatus* (Müller) occurs across the northern United States, and south in the Appalachians to North Carolina and on the Pacific coast to southern California, as well as in northern Europe, Africa, and Asia. It is one of the first psocids to mature in the spring. The female has very short wings, and the male is long-winged.

Family **Lachesillidae:** The members of this large family are inhabitants of persistent dead leaves of a great variety of plants. Some inhabit foliage of conifers, and others inhabit grasses. Although 54 species are now known in the United States, the number of species in Latin America is much larger.

Family **Peripsocidae:** This is one of two families in which there is no cubital loop in the fore wing; that is, vein Cu_1 is simple. The peripsocids are medium-sized inhabitants of twigs, branches, and trunks of conifers and broad-leaf trees. Some 14 species are now known in the United States.

Family **Ectopsocidae:** This is another family in which the cubital loop is absent in the fore wing. These are relatively small inhabitants of persistent dead leaves. *Ectopsocopsis cryptomeriae* (Enderlein) seems to thrive in agricultural situations where few other psocids exist. It occasionally invades food storage warehouses. Thirteen species of ectopsocids occur in the United States.

Family **Pseudocaeciliidae:** This is another family that shows pairs of crossing hairs on the posterodistal margin of the fore wing. North American species have two tarsal segments. Only three species occur in the United States, all probably introduced. *Pseudocaecilius citricola* (Ashmead) is a common yellow species on citrus trees in Florida.

Family **Trichopsocidae:** These are pale, delicate, leaf-inhabiting forms superficially resembling caeciliusids. Only two species occur in the United States; *Trichopsocus clarus* (Banks) is common in coastal California.

Family **Archipsocidae:** This is a third family in which there are pairs of crossing hairs on the posterodistal margin of the fore wing. This tropical family is restricted in North America to Florida, the Gulf Coast, and the Atlantic Coast north to South Carolina. Archipsocids are communal web-spinners. Males are short-winged, whereas females occur in short- and long-winged forms. About eight species occur in the United States.

Family **Hemipsocidae:** This is primarily a tropical family, with only two species in the United States, both in the Southeast. *Hemipsocus pretiosus* Banks lives on leaf litter and dead persistent leaves of small palms in southern Florida.

Family **Myopsocidae:** Although this group is largely tropical, it is represented in the fauna of North America by 10 species, all of which are 4–5 mm long and have mottled fore wings. They live on shaded stone outcrops and shaded cement structures, such as bridges, as well as tree trunks and branches.

Family **Psocidae:** This is the largest family in the United States, with some 75 species. Psocidae are moderate-sized to large psocids with the cubital loop always joined to M for a distance in the fore wing. Generally, they inhabit branches and trunks of various kinds of trees, foliage of conifers, and shaded rock outcrops. *Cerastipsocus venosus* Burmeister is a large, dark-colored species that forms herds of up to several hundred individuals on tree trunks and branches. It occurs throughout the eastern United States.

Collecting and Preserving Psocoptera

Psocids that live outdoors can often be collected by beating branches of trees and shrubs and sweeping grasses. Coniferous trees and fallen branches with persistent dead leaves often are sites where psocids are concentrated. Some species are found under loose bark, on stone outcrops, in ground litter, and in bird and mammal nests. Indoor species can be found in old papers and books, in stored grain and cereal products, and on wood surfaces in such sites as musty cellars. Individuals can be picked up with an aspirator or a small brush moistened with alcohol.

Psocids can be preserved in 70–80% alcohol, but some color fading will occur. Specimens mounted on pins or points keep their colors better, but they shrivel and must be restored in liquids for study.

It is often necessary to mount specimens or parts, such as legs, wings, mouthparts, and terminal abdominal segments, on microscope slides for study. For this, parts other than legs or wings should be partially cleared by soaking in a cold 10–15% aqueous solution of KOH for several minutes. They can then be washed in water and mounted in Hoyer's medium (see Chapter 35). Undigested material in the hindgut must be teased out with fine needles with the specimen under water.

References

Badonnel, A. 1951. Ordre des Psocoptères. In P. P. Grassé (Ed.), Traité de Zoologie, vol. 10, fasc. 2:1301–1340. Paris: Masson.

Chapman, P. J. 1930. Corrodentia of the United States of America. I. Suborder Isotecnomera. J. N.Y. Entomol. Soc. 39:54–65.

Eertmoed, G. E. 1966. The life history of *Peripsocus quadrifasciatus* (Psocoptera: Peripsocidae). J. Kan. Entomol. Soc. 39:54–65.

Eertmoed, G. E. 1973. The phenetic relationships of the Epipsocetae (Psocoptera): The higher taxa and the species of two new families. Trans. Amer. Entomol. Soc. 99:373–414.

Garcia Aldrete, A. N. 1974. A classification above species level of the genus *Lachesilla* Westwood (Psocoptera: Lachesillidae). Folia Entomol. Mex. 27:1–88.

Garcia Aldrete, A. N. 1999. New North American *Lachesilla* in the *forcepeta* group (Psocoptera Lachesillidae). Rev. Biol. Trop. 47:163–188.

Gurney, A. B. 1950. Corrodentia. In C. J. Weinman (Ed.), Pest Control Technology, Entomology Section, pp. 129–163. New York: National Pest Control Association.

Lee, S. S., and I. W. B. Thornton. 1967. The family Pseudocaeciliidae (Psocoptera)—A reappraisal based on the discovery of new Oriental and Pacific species. Pac. Insects Monogr. No. 18, 114 pp.

Lienhard, C. 1999. Faune de France 83. Psocoptères Euro-Mediterranéens. Fed. Franç. Soc. Sci. Nat. Paris, 517 pp.

Lienhard, C., and C. N. Smithers. 2002. Psocoptera (Insecta) World Catalogue and Bibliography. Instrumenta Biodiversitatis V. Geneva, Muséum d'Histoire Naturelle, 745 pp.

Mockford, E. L. 1957. Life history studies on some Florida insects of the genus *Archipsocus* (Psocoptera). Bull. Fla. State Mus. 1:253–274.

Mockford, E. L. 1959. The *Ectopsocus briggsi* complex in the Americas (Psocoptera: Peripsocidae). Proc. Entomol. Soc. Wash. 61:260–266.

Mockford, E. L. 1965. The genus *Caecilius* (Psocoptera: Caeciliidae). Part I: Species groups and the North American species of the *flavidus* group. Trans. Amer. Entomol. Soc. 91:121–166.

Mockford, E. L. 1966. The genus *Caecilius* (Psocoptera: Caeciliidae). Part II: Revision of the species groups, and the North American species of the *fasciatus*, *confluens*, and *africanus* groups. Trans. Amer. Entomol. Soc. 92:133–172.

Mockford, E. L. 1969. The genus *Caecilius* (Psocoptera: Caeciliidae). Part III: The North American species of the *alcinus*, *caligonus*, and *subflavus* groups. Trans. Amer. Entomol. Soc. 95:77–151.

Mockford, E. L. 1971a. Parthenogenesis in psocids (Insecta: Psocoptera). Amer. Zool. 11:327–339.

Mockford, E. L. 1971b. *Peripsocus* species of the *alboguttatus* group (Psocoptera: Peripsocidae). J. N.Y. Entomol. Soc. 79:89–115.

Mockford, E. L. 1978. A generic classification of family Amphipsocidae (Psocoptera: Caecilietae). Trans. Amer. Entomol. Soc. 104:139–190.

Mockford, E. L. 1987. Order Psocoptera In F. W. Stehr (Ed.), Immature Insects, pp. 196–214. Dubuque, IA: Kendall/Hunt, 754 pp.

Mockford, E. L. 1987. Systematics of North American and Greater Antillean species of *Embidopsocus* (Psocoptera: Liposcelidae). Ann. Entomol. Soc. Amer. 80:849–864.

Mockford, E. L. 1989. *Xanthocaecilius* (Psocoptera: Caeciliidae), a new genus from the Western Hemisphere. I: Description, species complexes and species of the *quillayute* and *granulosus* complexes. Trans. Amer. Entomol. Soc. 114:265–294.

Mockford, E. L. 1993. North American Psocoptera (Insecta). Flora and Fauna Handbook No. 10. Gainesville, FL: Sandhill Crane Press, 455 pp.

Mockford, E. L. 1998. Generic definitions and species assignments in the family Epipsocidae (Psocoptera). Insecta Mundi 12:81–91.

Mockford, E. L. 2000. A classification of the psocopteran family Caeciliusidae (Caeciliidae Auct.). Trans. Amer. Entomol. Soc. 125:325–417.

Mockford, E. L., and A. B. Gurney. 1956. A review of the psocids, or book-lice and bark-lice, of Texas (Psocoptera). J. Wash. Acad. Sci. 46:353–368.

Mockford, E. L., and D. M. Sullivan. 1986. Systematics of the graphocaeciliine psocids with a proposed higher classification of the family Lachesillidae (Psocoptera). Trans. Amer. Entomol. Soc. 112:1–80.

Mockford, E. L., and D. M. Sullivan. 1990. *Kaestneriella* Roesler (Psocoptera: Peripsocidae): New and little-known species from the southwestern United States and Mexico and a revised key. Pan-Pac. Entomol. 66:281–291.

New, T. R. 1974. Psocoptera. Roy. Entomol. Soc. Lond. Handbooks Identif. Brit. Insects 1(7):1–102.

New, T. R. 1987. Biology of the Psocoptera. Oriental Insects 21:1–109.

Pearman, J. V. 1928. On sound production in the Psocoptera and on a presumed stridulatory organ. Entomol. Mon. Mag. 64:179–186.

Pearman, J. V. 1936. The taxonomy of the Psocoptera; preliminary sketch. Proc. Roy. Entomol. Soc. Lond. Ser. B, 5(3):58–62.

Roesler, R. 1944. Die Gattungen der Copeognathen. Stn. Entomol. Ztg. 105:117–166.

Smithers, C. N. 1967. A catalog of the Psocoptera of the world. Austral. Zool. 14:1–145.

Smithers, C. N. 1972. The classification and phylogeny of the Psocoptera. Austral. J. Zool. 14:1–349.

Smithers, C. N., and C. Lienhard. 1992. A revised bibliography of the Psocoptera (Arthropoda: Insecta). Tech. Rept. Australian Mus. No. 6:1–86.

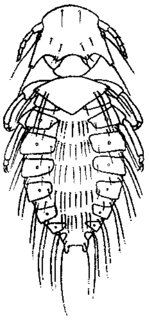
Sommerman, K. M. 1943. Bionomics of *Ectopsocus pumilis* (Banks) (Corrodentia: Caeciliidae). Psyche 50:55–63.

Sommerman, K. M. 1944. Bionomics of *Amapsocus amabilis* (Walsh) (Corrodentia: Psocidae). Ann. Entomol. Soc. Amer. 37:359–364.

Sommerman, K. M. 1946. A revision of the genus *Lachesilla* north of Mexico (Corrodentia; Caeciliidae). Ann. Entomol. Soc. Amer. 39:627–661.

25

Order Phthiraptera[1,2]
Lice



The lice are small, wingless ectoparasites of birds and mammals. These insects formerly were divided into two separate orders, the Mallophaga (chewing lice) and Anoplura (sucking lice). The suborder Anoplura contains several species that are parasites of domestic animals and two species that attack humans. These insects are irritating pests, and some are important vectors of disease. Many chewing lice (suborders Amblycera and Ischnocera) are pests of domestic animals, particularly poultry. These lice cause considerable irritation, and heavily infested animals appear run-down and emaciated. If not actually killed by the lice, they are still easy prey for disease. Different species of lice attack different types of poultry and domestic mammals, and each species usually infests a particular part of the host's body. None of the chewing lice is known to attack people. Those who handle birds or other infested animals may occasionally get the lice on themselves, but the lice do not stay long. The control of chewing lice usually involves treating the infested animal with a suitable dust or dip. A third suborder of chewing lice, the Rhynchophthirina, contains only three species, parasites of the elephants and some African pigs.

The Anoplura feed on the blood of their host. The mouthparts of a sucking louse consist of three piercing stylets that are normally withdrawn into a stylet sac in the head (Figure 25–1). The mouthparts are highly specialized and difficult to homologize with those of other insects. There is a short rostrum (probably the labrum) at the anterior end of the head, from which the three piercing stylets are protruded. The rostrum is eversible and is armed internally with small, recurved teeth. The stylets are about as long as the head and, when not in use, are withdrawn into a long, saclike structure below the alimentary canal. The dorsal stylet probably represents the fused maxillae. Its edges are curved upward and inward to form a tube that serves as a food channel. The intermediate stylet is very slender and contains the salivary channel; this stylet is probably the hypopharynx. The ventral stylet is the principal piercing organ; it is a trough-shaped structure and is probably the labium. There are no palps.

When an anopluran feeds, the stylets are everted through a rostrum at the front of the head. The rostrum has tiny hooks with which the louse attaches to its host while feeding. The chewing lice have mandibulate mouthparts and feed on bits of hair, feathers, or skin of the host. Ocelli are absent, and eyes are usually reduced or absent. The antennae are short and have three to five segments.

The tarsi of sucking lice are one-segmented and have a single, large claw that usually fits against a thumblike process at the end of the tibia. This forms an efficient mechanism for hanging to the hairs of the host.

The Phthiraptera undergo simple metamorphosis. The females of most species lay from 50 to 150 eggs, nearly always attaching them to the hairs or feathers of the host. The eggs usually hatch in about a week, and in most species the developing louse goes through three nymphal instars.

Classification of the Phthiraptera

Entomologists disagree on the higher classification of the lice. Most researchers now recognize a single order, the Phthiraptera, with four suborders (one being the Anoplura). The sucking lice clearly form a distinct

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[1] Phthiraptera: *phthir*, lice; *a*, without; *ptera*, wings.

[2] This chapter was edited by Ronald A. Hellenthal and Roger D. Price.

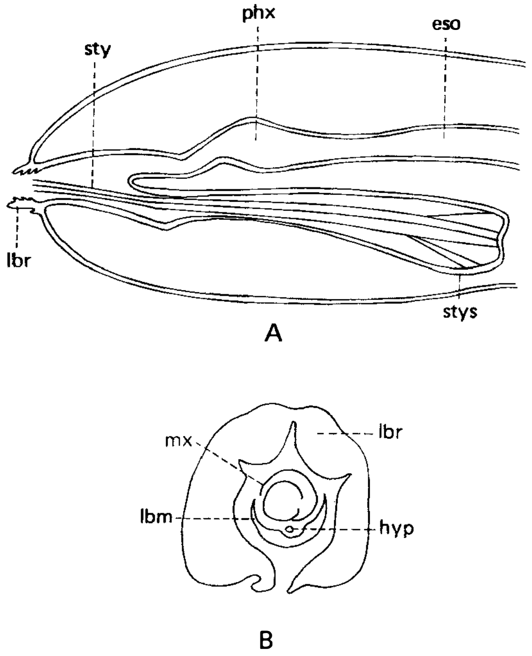


Figure 25–1 Mouthparts of a sucking louse. A, sagittal section of head; B, cross section through rostrum. *eso*, esophagus; *hyp*, intermediate stylet (probably hypopharynx); *lbm*, ventral stylet (probably labium); *lbr*, rostrum (probably labrum); *mx*, dorsal stylet (probably the fused maxillae); *phx*, pharynx; *sty*, stylets; *stys*, stylet sac. (Redrawn from Snodgrass.)

phylogenetic branch and deserve separate recognition at some level. It is the classification of the chewing lice that causes problems. Kim and Ludwig (1978b, 1982) have hypothesized that the characteristics that distinguish lice from their closest relatives, the Psocoptera, have evolved numerous times in parallel as a result of the ectoparasitic niche they occupy; therefore Kim and Ludwig advocate recognizing two orders, Mallophaga and Anoplura. However, the relationships among the suborders of lice are poorly understood. Kim and Ludwig (1982) summarize the evidence for and against several alternative schemes. The only common element is that all lice together form a monophyletic unit whose sister group is the Psocoptera. Until the phylogeny is better understood, we will recognize a single order of lice, the Phthiraptera. We follow here the familial classification of Kim et al. (1986) within the suborder Anoplura and follow Price et al. (2003) for the other suborders. These groups, with synonyms and other arrangements in parentheses, are as follows:

Suborder Rhynchophthirina (Mallophaga in part)
  Haematomyzidae—lice of elephants and African pigs

Suborder Amblycera (Mallophaga in part)
  Gyropidae (including Abrocomophagidae)—lice of guinea pigs
  Trimenoponidae—lice of chinchillas, guinea pigs, and Neotropical mammals
  Boopiidae (Boopidae)—lice of marsupials and dogs
  Menoponidae—lice of birds
  Laemobothriidae—lice of birds
  Ricinidae—lice of birds

Suborder Ischnocera (Mallophaga in part)
  Philopteridae (including Heptapsogasteridae)—lice of birds
  Trichodectidae—lice of mammals

Suborder Anoplura
  Echinophthiriidae—lice of seals, sea lions, walruses, and the river otter
  Enderleinellidae (Hoplopleuridae in part)—lice of squirrels
  Haematopinidae—lice of ungulates (pigs, cattle, horses, deer)
  Hoplopleuridae—lice of rodents and insectivores
  Linognathidae—lice of even-toed ungulates (cattle, sheep, goats, deer) and canids (dogs, foxes, coyotes)
  Pecaroecidae—lice of peccaries
  Pediculidae—the head and body lice of humans
  Polyplacidae (Hoplopleuridae in part)—lice of rodents and insectivores
  Pthiridae (Phthiridae, Phthiriidae)—the crab louse of humans

Key to the Families of Phthiraptera

1.	Head prolonged into snout with apical mandibles (parasitic on elephants and African porcines) (Suborder Rhynchophthirina)	**Haematomyzidae**	p. 361
1′.	Head not prolonged into snout with apical mandibles	2	

2(1′). Head as wide as or wider than prothorax (Figures 25–2 through 25–4); mouthparts mandibulate; parasites of birds (with 2 tarsal claws) and mammals (with 1 tarsal claw) 3

2′. Head usually narrower than prothorax (Figures 25–5, 25–6); mouthparts haustellate; parasites of mammals, with 1 large tarsal claw (Suborder Anoplura) 10

3(2). Antennae more or less clubbed and usually concealed in grooves; maxillary palps present (Figure 25–2A and 25–3) (Suborder Amblycera) 4

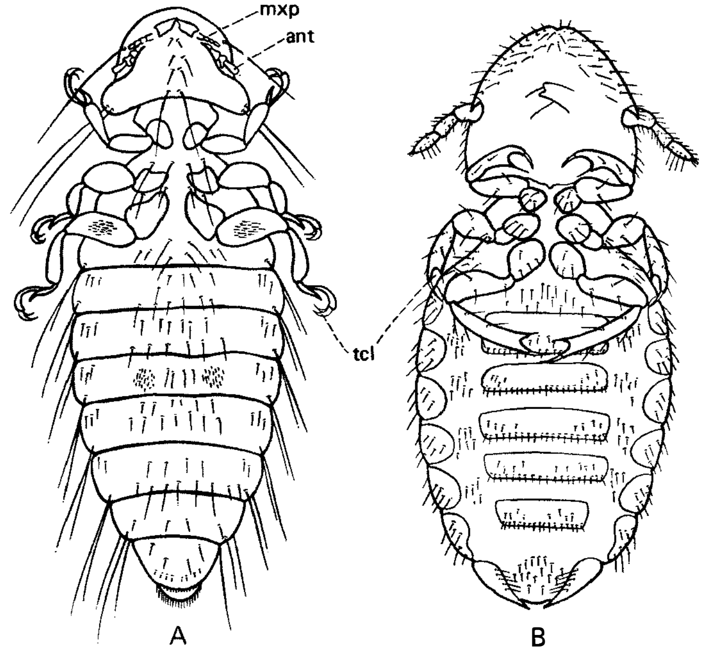


Figure 25–2 A, shaft louse of chickens, *Menopon gallinae* (L.) (Menoponidae); ventral view of female; B, cattle-biting louse, *Bovicola bovis* (L.) (Trichodectidae), ventral view of female. *ant*, antenna; *mxp*, maxillary palp; *tcl*, tarsal claws.

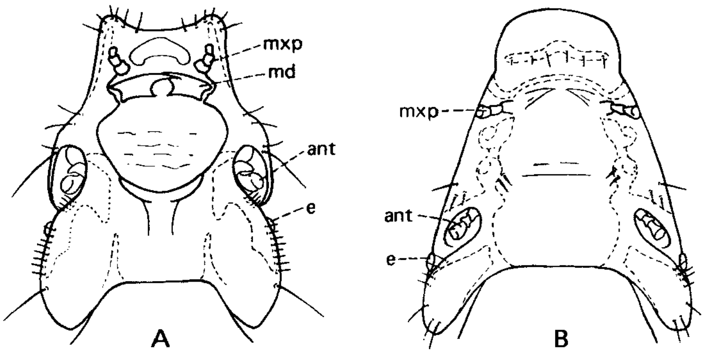


Figure 25–3 A, head of *Laemobothrion* (Laemobothriidae), ventral view; B, head of a ricinid (Ricinidae), ventral view. *ant*, antenna; *e*, eye; *md*, mandible; *mxp*, maxillary palp.

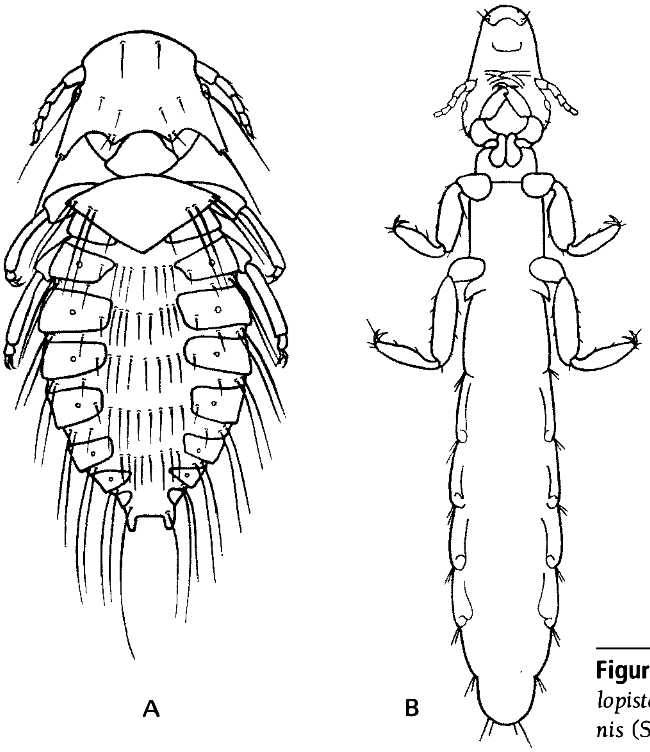


Figure 25–4 Philopteridae. A, the large turkey louse, *Chelopistes meleagridis* (L.), dorsal view; B, *Anaticola crassicornis* (Scopoli), a louse of the blue-winged teal, ventral view.

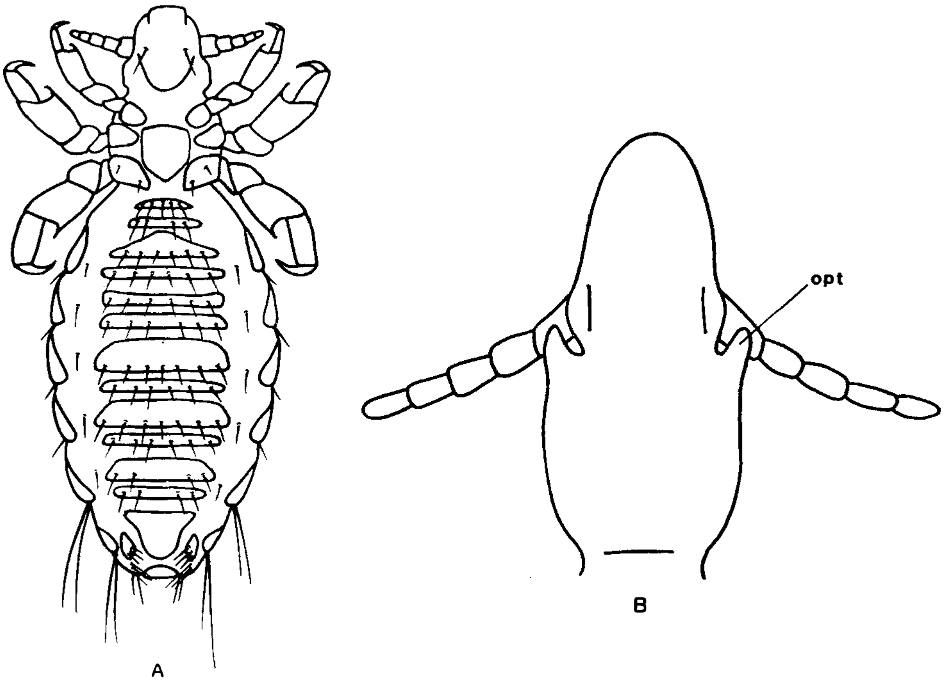


Figure 25–5 A, the spined rat louse, *Polyplax spinulosa* (Burmeister), female, ventral view (Polyplacidae); B, head of the hog louse, *Haematopinus suis* (L.), dorsal view (Haematopinidae). *opt*, ocular point.

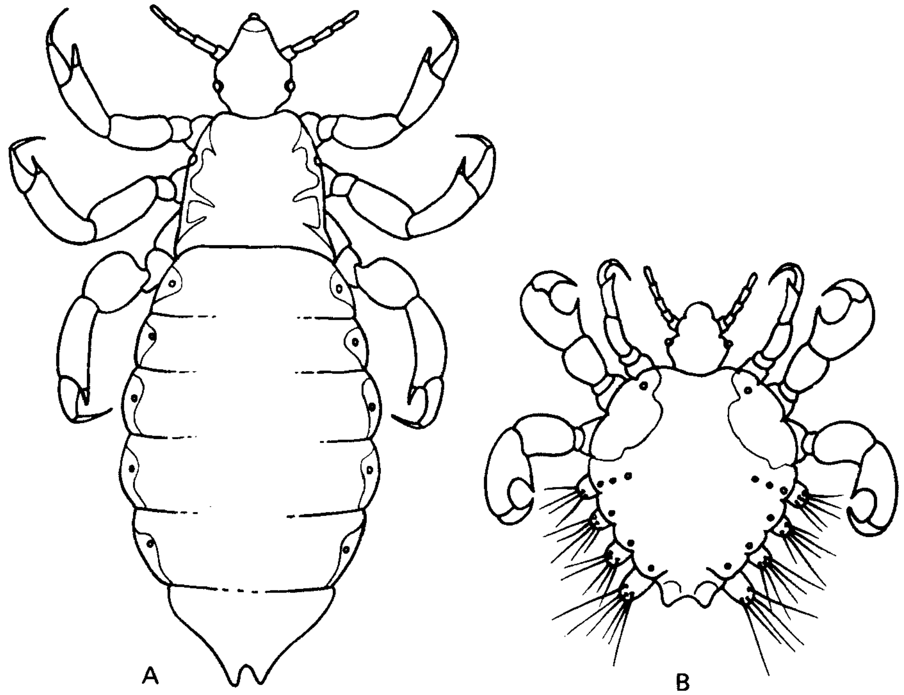


Figure 25–6 Human lice. A, the body louse, female; B, the crab louse, female. 20×.

3′.	Antennae filiform and exposed; maxillary palps absent (Figures 25–2B and 25–4) (Suborder Ischnocera)	9	
4(3).	With 1 tarsal claw or none; parasitic on guinea pigs	Gyropidae	p. 361
4′.	With 2 tarsal claws; parasitic on birds, marsupials, and dogs	5	
5(4′).	With only 5 pairs of abdominal spiracles; parasitic on guinea pigs, chinchillas, and New World marsupials, except for North American opossums	Trimenoponidae	p. 361
5′.	With 6 pairs of abdominal spiracles	6	
6(5′).	Antennae 5-segmented and strongly clubbed; legs long and slender; parasitic on Australian marsupials and dogs	Boopiidae	p. 361
6′.	Antennae 4-segmented and less strongly clubbed; legs not particularly long and slender; parasitic on birds	7	
7(6′).	Antennae in grooves on sides of head; head broadly triangular and expanded behind eyes (Figure 25–2A)	Menoponidae	p. 361
7′.	Antennae in cavities that open ventrally; head *not* broadly triangular and expanded behind eyes (Figure 25–3)	8	
8(7′).	Sides of head with conspicuous swelling in front of eye at base of antenna (Figure 25–3A)	Laemobothriidae	p. 361
8′.	Sides of head without such swelling (Figure 25–3B)	Ricinidae	p. 361
9(3′).	Tarsi with 2 claws; antennae 5-segmented (Figure 25–4); parasitic on birds	Philopteridae	p. 362
9′.	Tarsi with 1 claw; antennae usually 3-segmented (Figure 25–2B); parasitic on mammals	Trichodectidae	p. 362
10(2′).	Head with distinct eyes (Figure 25–6) or with subacute ocular points on sides of head behind antennae (Figure 25–5B, opt)	11	

10′.	Head without eyes or prominent ocular points (Figure 25–5A)	14	
11(10).	Head with eyes but without ocular points (Figure 25–6); parasites of humans and peccaries	12	
11′.	Head without eyes but with prominent ocular points (Figure 25–5B, opt); parasites of ungulates	**Haematopinidae**	p. 362
12(11).	Head long and slender, much longer than thorax; southwestern United States, on peccaries	Pecaroecidae	p. 362
12′.	Head about as long as thorax (Figure 25–6); parasites of humans	13	
13(12′)	Abdomen about as long as its basal width, and with prominent lateral lobes (Figure 25–6B); middle and hind legs stouter than front legs	**Pthiridae**	p. 363
13′.	Abdomen much longer than its basal width, and without lateral lobes (Figure 25–6A); middle and hind legs not stouter than front legs	**Pediculidae**	p. 362
14(10′).	Body thickly covered with short, stout spines, abdomen with scales; parasites of seals, walrus, and river otter	**Echinophthiriidae**	p. 362
14′.	Body with only a few setae, abdomen without scales; parasites of terrestrial mammals	15	
15(14′).	Front and middle legs similar in size and shape, both smaller, more slender than hind legs; parasites of squirrels	**Enderleinellidae**	p. 362
15′.	Front legs smallest of the three pairs, middle and hind legs similar in size and shape (Figure 25–5A), or hind legs larger; parasites of ungulates, canids, rodents, and insectivores	16	
16(15′).	Front coxae widely separated; parasites of even-toed ungulates and canids	**Linognathidae**	p. 362
16′.	Front coxae contiguous or nearly so; parasites of rodents and insectivores	17	
17(16′).	Hind legs largest of the 3 pairs; sternite of second abdominal segment extending laterally on each side to articulate with the tergite	**Hoplopleuridae**	p. 362
17′.	Middle and hind legs similar in size and shape (Figure 25–5A); sternite of second abdominal segment not extending laterally on each side and not articulating with tergite	**Polyplacidae**	p. 363

Family **Haematomyzidae:** The three species in this group are found on Asian and African elephants, the wart hog, and the African bush pig. Its distinctive elongated head is unique among the Phthiraptera. It is found both on wild elephants and those that have long been in captivity.

Family **Gyropidae:** The members of this group are chiefly confined to Central and South America. Two species occur in the United States on guinea pigs. *Pitrufquenia coypus* Marelli has been collected from feral nutria in the southeastern United States. *Macrogyropus dicotylis* (Macalister) lives on the collared peccary.

Family **Trimenoponidae:** All but a single species are restricted to Neotropical rodents and marsupials. *Trimenoponon hispidum* (Burmeister) occurs on the guinea pig and, with its host, now has a worldwide distribution.

Family **Boopiidae:** This group is represented in the United States by one species: *Heterodoxus spiniger* Enderlein, which lives on dogs and coyotes in the southwestern states. It is an intermediate host to several internal parasites of canids. Most members of this family occur in Australia, where they are parasites of marsupials.

Family **Menoponidae:** This is a large group whose members attack birds. Two important pests of poultry in this group are the chicken body louse, *Menacanthus stramineus* (Nitzsch), and the shaft louse, *Menopon gallinae* (L.) (Figure 25–2A).

Family **Laemobothriidae:** This is a small group of very large lice whose members are parasites of water birds and birds of prey. Eight species, all in the genus *Laemobothrion*, occur in the United States.

Family **Ricinidae:** This is a small group whose members are parasites of birds, including hummingbirds and passerine birds.

Family **Philopteridae:** This is the largest family in the order and contains species parasitizing a wide variety of birds. Two important pests of poultry in this group are the chicken head louse, *Cuclotogaster heterographus* (Nitzsch), and the large turkey louse, *Chelopistes meleagridis* (L.) (Figure 25–4A).

Family **Trichodectidae:** The trichodectids are parasites of mammals. Some important pest species in this group are the cattle-biting louse, *Bovicola bovis* (L.) (Figure 25–2B); the horse-biting louse, *Bovicola (Werneckiella) equi* (Denny); and the dog-biting louse, *Trichodectes canis* (DeGeer).

Family **Echinophthiriidae:** The five North American species in this group attack aquatic mammals (seals, and the sea lion, walrus, and the river otter). At least some species burrow into the skin of their host.

Family **Enderleinellidae:** This is a widely distributed group, with 10 North American species, whose members are parasites of squirrels. They may be recognized by the fact that the front and middle legs are similar in size and more slender than the hind legs. Most North American species belong to the genus *Enderleinellus*. *Microphthirus uncinatus* (Ferris), a parasite of flying squirrels, is shorter than 0.5 mm and is the smallest louse in this order.

Family **Haematopinidae:** The lice in this group attack pigs, cattle, horses, and deer. They differ from other sucking lice in having ocular points on the sides of the head behind the eyes (Figure 25–5B, opt). This family contains four North American species, including the hog louse, *Haematopinus suis* (L.); the horse-sucking louse, *H. asini* (L.); and two species of *Haematopinus* that attack cattle.

Family **Hoplopleuridae:** The members of this group (17 North American species) attack rodents, hares, moles, and shrews. These lice differ from other Anoplura attacking these hosts (Polyplacidae) in the form of the sternite of the second abdominal segment and the relative size of the different legs (see key, couplet 17).

Family **Linognathidae:** This group includes 10 North American species that are parasites of cattle, sheep, goats, deer, reindeer, dogs, coyotes, and foxes. It includes the dog-sucking louse, *Linognathus setosus* (Olfers); the goat-sucking louse, *L. stenopsis* (Burmeister); and the long-nosed cattle louse, *L. vituli* (L.). The last species differs from the haematopinids attacking cattle in lacking ocular points on the head.

Family **Pecaroecidae:** This group includes a single North American species, *Pecaroecus jayvalii* Babcock and Ewing, which occurs in the Southwest on peccaries. This species is the largest North American anopluran, and can reach a length of 8 mm.

Family **Pediculidae:** This group includes the head and body lice of humans, *Pediculus humanus capitis* DeGeer and *P. h. humanus* L., respectively, which are considered subspecies of a single species, *P. humanus*. These lice (Figure 25–6A) are narrower and more elongate than crab lice. The head is only a little narrower than the thorax, and the abdomen lacks lateral lobes. Adults are 2.5 to 3.5 mm long.

The head and body lice have a similar life history, but differ somewhat in habits. The head louse occurs chiefly on the head, and its eggs are attached to the hair. The body louse occurs primarily on the body, and its eggs are laid on clothing, particularly along the seams. The eggs hatch in about a week, and the entire life cycle from egg to adult requires about a month. Lice feed at frequent intervals, and individual feedings last a few minutes. Body lice usually hang onto clothing while feeding, and often remain on clothing when it is removed. The head louse is transmitted from person to person through the exchange of combs, hair brushes, and caps or hats. The body louse is transmitted by clothing and bedding, and at night may migrate from one pile of clothes to another.

The body louse (also called "cootie" or "seam squirrel") is an important vector of human disease. The most important disease it transmits is epidemic typhus, which may occur in outbreaks in war or famine conditions, sometimes with a high mortality rate. Body lice become infected by feeding on a typhus patient and can infect another person a week or so later. Infection results from scratching the feces of the louse, or the crushed louse itself, into the skin. This disease is not transmitted by the louse bite. Another important louse-borne disease is a type of relapsing fever that is transmitted by the infected louse being crushed and rubbed into the skin. Neither the feces nor the bite of the louse is infective. A third louse-borne disease is trench fever, which occurred in epidemic proportions during World War I, but since then has not been very important.

People who bathe and change clothes regularly seldom become infested with lice, but when they go for long periods without doing so and live in crowded conditions, lousiness is likely to be prevalent. The latter conditions are often common during wartime, when living quarters are crowded and people go for long periods without a change of clothes. If a louse-borne disease such as typhus gets started in a population that is heavily infested with body lice, it can quickly swell into an epidemic.

The control of body lice usually involves dusting people with an insecticide. Clothing must also be treated, because the eggs are laid on it, and adult lice often cling to clothing when it is removed. The treatment of clothing usually involves chemical fumigation or heat sterilization.

Epidemics of typhus have raged in many military campaigns and have often caused more casualties than actual combat. Until World War II, there were no simple and easily applied controls for body lice. DDT, which first came into use during this war, proved ideal for louse control. In the fall of 1943, when a typhus epidemic threatened Naples, Italy, dusting thousands of people with DDT brought the epidemic under complete control in only a few months. In the years since then, body lice have developed resistance to DDT, and this insecticide is no longer as effective in their control as it used to be.

Family **Polyplacidae:** This family is the largest family in the suborder, with 26 North American species. Its members attack rodents, hares, moles, and shrews. Some species in other parts of the world attack primates (monkeys and lemurs).

Family **Pthiridae:** The only member of this family in North America is the crab louse of humans, *Pthirus pubis* (L.) (Figure 25–6B), but there is also an African species (*P. gorillae* Ewing) that attacks gorillas. *Pthirus pubis* is broadly oval and somewhat crab-shaped, with the claws of the middle and hind legs very large, the head much narrower than the thorax, and the abdominal segments with lateral lobes. Adults are 1.5 to 2.0 mm long. This louse occurs chiefly in the pubic region, but in hairy people may occur almost anywhere on the body. The eggs (nits) are attached to body hairs. The crab louse is an irritating pest, but is not known to transmit any disease.

Collecting and Preserving Phthiraptera

The only effective way to find lice is to examine their hosts carefully. Hosts other than domestic animals usually must be shot or trapped. Lice often are found still attached to museum skins of birds or mammals. Small host animals collected in the field to be examined later should be placed in a tightly closed bag. Any lice that fall or crawl off the host can then be found in the bag. To be certain of the host relationship, place different species, or preferably different individuals, of the host in separate bags.

Examine all parts of the host, because different species of lice often occur on different parts of the same host. The best way to locate lice is to go over the host carefully with forceps, or a comb can often be used to advantage. The lice sometimes fall off if the host is shaken over a sheet of paper. Lice may be picked up with forceps or with a camel's-hair brush moistened with alcohol.

Preserve lice in 70–75% alcohol, along with collection and host data. Use a different vial for the lice from each host. Collection data (on a label inside the vial) should include the host species, the date, the locality, and the name of the collector.

Lice must be mounted on microscope slides for detailed study; specimens preserved on pins or points are unsatisfactory. Specimens to be mounted are first cleared for a day or so in cold KOH. It is sometimes desirable to stain the specimen before mounting it on a slide. Kim et al. (1986, pp. 3–5) give detailed directions for collecting and mounting Anoplura.

References

Clay, T. 1970. The Amblycera (Phthiraptera: Insecta). Bull. Brit. Mus. (Nat. Hist.) Entomol. 25:73–98.

Cruickshank, R. H., K. P. Johnson, V. S. Smith, R. J. Adams, D. H. Clayton, and R. D. M. Page. 2001. Phylogenetic analysis of partial sequences of elongation factor 1 alpha identifies major groups of lice (Insecta: Phthiraptera). Mol. Phylog. Evol. 19:202–215.

Durden, L. A., and G. G. Musser. 1994a. The sucking lice (Insecta: Anoplura) of the world: A taxonomic checklist with records of mammalian hosts and geographical distribution. Bull. Amer. Mus. Nat. Hist. 218:1–90.

Durden, L. A., and G. G. Musser. 1994b. The mammalian hosts of the sucking lice (Anoplura) of the world: A host–parasite list. Bull. Soc. Vector Ecol. 19:130–168.

Ferris, G. F. 1951. The sucking lice. Mem. Pac. Coast Entomol. Soc. 1:1–321.

Hopkins, G. H. E., and T. Clay. 1952. A Check List of the Genera and Species of Mallophaga. London: British Museum (Natural History), 362 pp.

Kim, K. C. (Ed.). 1985. Coevolution of parasitic arthropods and mammals. New York: Wiley, 800 pp.

Kim, K. C. 1987. Order Anoplura. In F. W. Stehr (Ed.), Immature Insects, pp. 224–245. Dubuque, IA: Kendall/Hunt, 754 pp.

Kim, K. C., and H. W. Ludwig. 1978a. The family classification of the Anoplura. Syst. Entomol. 3:249–284.

Kim, K. C., and H. W. Ludwig. 1978b. Phylogenetic relationships of parasitic Psocodea and taxonomic position of the Anoplura. Ann. Entomol. Soc. Amer. 71:910–922.

Kim, K. C., and H. W. Ludwig. 1982. Parallel evolution, cladistics, and classification of parasitic Psocodea. Ann. Entomol. Soc. Amer. 75:537–548.

Kim, K. C., H. D. Pratt, and C. J. Stojanovich. 1986. The sucking lice of North America. University Park: Pennsylvania State University Press, 241 pp.

Lyal, C. H. C. 1985. A cladistic analysis and classification of trichodectid mammal lice (Phthiraptera: Ischnocera). Bull. Brit. Mus. (Nat. Hist.) Entomol. 51:187–346.

Price, M. A., and O. H. Graham. 1997. Chewing and sucking lice as parasites of mammals and birds. U.S. Dept. Agric. Tech. Bull. 1849. 309 pp.

Price, R. D. 1987. Order Mallophaga. In F. W. Stehr (Ed.), Immature Insects, pp. 215–223. Dubuque, IA: Kendall/Hunt, 754 pp.

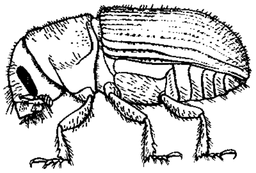
Price, R. D., R. A. Hellenthal, R. L. Palma, K. P. Johnson, and D. H. Clayton. 2003. The chewing lice: World checklist and biological overview. Illinois Nat. Hist. Surv. Special Publ. 24. Champaign, IL: Illinois Natural History Survey, 458 pp.

Werneck, F. L. 1948–1950. Os Malófagos de Mamiferos. Parte I. Amblycera e Ischnocera (Philopteridae e parte de Trichodectidae), 243 pp. (1948). Parte II: Ischnocera (continuação de Trichodectidae) e Rhynchophthirina. 207 pp. (1950). Rio de Janeiro: Edição da Revista Brasileira de Biologia.

26

Order Coleoptera[1,2]

Beetles



The Coleoptera are the largest order of insects, with about 40% of the known species in the Hexapoda. More than a quarter of a million beetle species have been described, and about 30,000 of these occur in the United States and Canada. These vary in length (in the United States) from less than a millimeter up to about 75 mm. Some tropical species reach a length of about 125 mm. The beetles vary considerably in habits and are found almost everywhere. Many species are of great economic importance.

One of the most distinctive features of the Coleoptera is the structure of the wings. Most beetles have four wings, with the front pair thickened, leathery, or hard and brittle. Called *elytra* (singular, *elytron*), these front wings usually meet in a straight line down the middle of the back and cover the hind wings (hence the order name). The hind wings are membranous, are usually longer than the front wings, and at rest are usually folded up under the front wings (Figure 26–1). The elytra normally serve as protective sheaths and are held motionless during flight, which is powered by the hind wings. The front or hind wings are greatly reduced in a few beetles.

The mouthparts in this order are of the chewing type, and the mandibles are well developed. The mandibles of many beetles are stout and are used in crushing seeds or gnawing wood. In others, they are slender and sharp. In the weevils, the front of the head is drawn out into a more or less elongated snout with the mouthparts at the end.

The beetles undergo complete metamorphosis. The larvae vary considerably in form in different families. Most beetle larvae are campodeiform or scarabaeiform, but some are platyform, some are elateriform, and a few are vermiform.

Beetles may be found in almost every type of habitat that is inhabited by insects, and they feed on all sorts of plant and animal materials. Many are phytophagous, predaceous, or fungivorous, whereas some are scavengers and a very few are parasitic. Some are subterranean in habit; many are aquatic or semiaquatic; and a few live as commensals in the nests of social insects or mammals. Some of the phytophagous species are free feeders on foliage, and others bore into wood or fruits or live as leaf miners. Others attack roots, and some feed on parts of blossoms or on pollen. Any part of a plant may be fed on by some type of beetle. Many beetles feed on

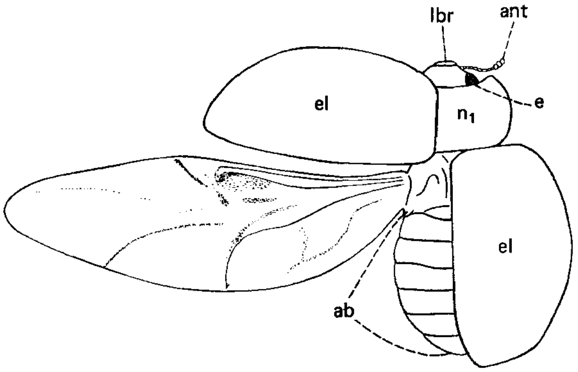


Figure 26–1 Dorsal view of a ladybird beetle (*Adalia* sp.), with the left wings extended. *ab*, abdomen, *ant*, antenna; *e*, compound eye; *el*, elytron; *lbr*, labrum; *n_1*, pronotum.

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[1] Coleoptera: *coleo*, sheath; *ptera*, wings (referring to the elytra).

[2] The section on Chrysomelidae was edited by Shawn Clark, and the section on Curculionoidea was edited by Robert S. Anderson.

stored plant or animal products, including many types of foods, clothing, and other organic materials. One Californian species is infamous for its ability to bore through the lead sheathing once used on telephone cables. Many beetles are of value to humans because they destroy injurious insects or act as scavengers.

The life cycle in this order varies in length from four generations a year to one generation in several years. Most species have one generation a year. The winter may be passed in any of the life stages, depending on the species. Many overwinter as partly grown larvae, pupae in chambers in soil, wood, or other protected situations; and many overwinter as adults. Relatively few species overwinter as eggs.

Sound Production in the Coleoptera

Sound production has been reported in about 50 families of Coleoptera, but the sounds are generally rather weak and have been much less studied than the sounds of Orthoptera and cicadas. Relatively little is known of the role these sounds play in behavior.

Beetles produce sounds in four principal ways: (1) in the course of normal activities such as flying and feeding; (2) by striking some part of the body against the substrate; (3) by stridulation; and (4) chemically.

Flight sounds, produced by the movements of the wings, are similar to those produced by other flying insects. Feeding sounds depend on the size of the beetles and the material fed on, but in some cases these sounds may be fairly loud. A large wood-boring beetle larva feeding in a log can sometimes be heard from several feet away. Feeding sounds, such as those of wood-boring larvae or grain-feeding beetles, probably play no role in communication from one beetle to another but do indicate (communicate) to humans presence (and feeding) of the insects.

Adult deathwatch beetles (*Anobium* and *Xestobium* spp., family Anobiidae) make sounds by striking the lower parts of their heads against the walls of their galleries (in wood). In quiet surroundings, these sounds are quite apparent. In Arizona and California, adults of *Eupsophulus castaneus* Horn (Tenebrionidae) cause some annoyance by tapping their abdomens against screen doors and windows, producing a surprisingly loud noise. Another tenebrionid, *Eusattus reticulatus* (Say), produces a sound by rapidly tapping the apex of the abdomen against the ground.

When a click beetle on its back "jumps" (see page 422), there is a distinct clicking sound. It is not clear whether the click is caused by the body striking the substrate or the prosternal peg stopping abruptly in the mesosternal notch.

In the Coleoptera, most sounds, including the sounds that may be involved in communication, are produced by stridulation. The stridulatory structures may be located on almost any part of the body and involve an area bearing a series of ridges (the "file") and a "scraper," usually a hard ridge, knob, or spine, which is rubbed against the file. Most stridulatory structures are on adults, but in a few beetle species the larvae, or even the pupae, stridulate.

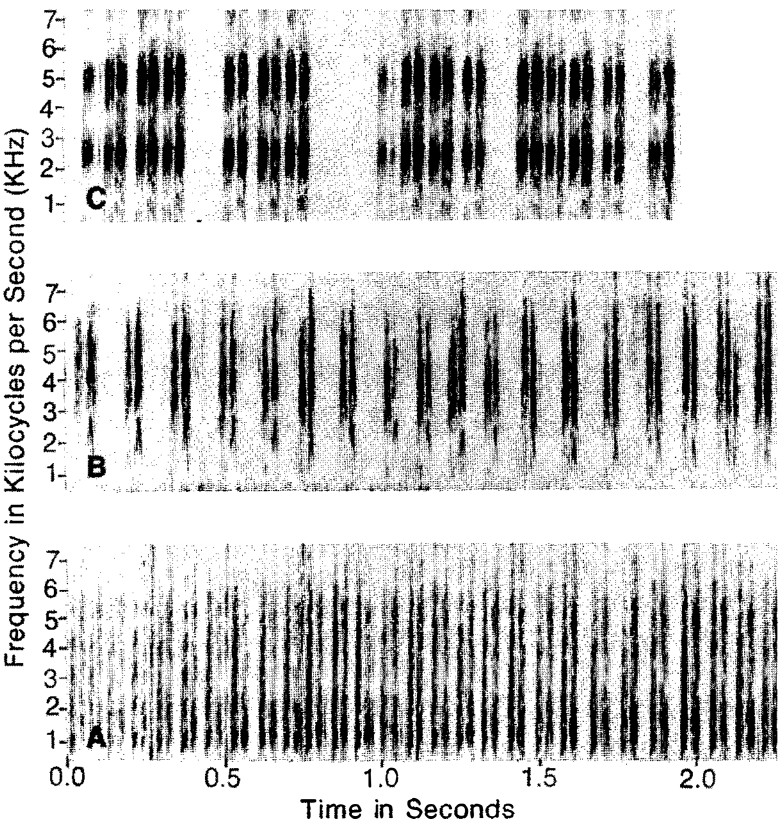
The stridulatory structures in beetles may involve the head and pronotum (Nitidulidae, Tenebrionidae, Endomychidae, Curculionidae), head appendages (usually mouthparts; certain Scarabaeidae), pronotum and mesonotum (common in the Cerambycidae), leg and thorax (Anobiidae, Bostrichidae), leg and abdomen (some Scarabaeidae), leg and leg (adult and larval Passalidae, Lucanidae, and some Scarabaeidae), abdomen and hind wings (Passalidae), and elytra and abdomen (Hydrophilidae, Curculionidae).

Beetle stridulations are produced in four general sorts of situations: (1) when the insect is handled or attacked ("stress" sounds); (2) in aggressive situations, such as fighting; (3) in calling (attracting the opposite sex); and (4) prior to mating (a "courtship" sound). Probably most beetles that stridulate produce stress sounds, and such sounds may help deter potential predators. Stress sounds may be the only ones some beetles produce, whereas other beetles (for example, the hydrophilid genus *Berosus* and bark beetles) may produce other types of sounds.

Another type of sound is produced by ground beetles (Carabidae) of the genus *Brachinus*. Two chemicals held in reservoirs at the end of the abdomen are expelled at the same time, and mix in the air to create a chemical reaction releasing heat. This produces a distinctive popping sound, like a tiny explosion, which probably deters predators.

Beetle sounds vary in their character, depending on the species and how the sounds are produced, but most are of a quality that might be described as a chirp, a squeak, or a rasping sound. Most contain a broad band of frequencies (Figure 26–2). Stress sounds and some aggressive sounds are generally produced at an irregular rate of, at most, only a few per second. In calling and courtship sounds, the chirps are produced at a faster, regular rate, which differs in different species (Figure 26–2).

The sounds produced by beetles in the genus *Berosus* (Hydrophilidae) are of two sorts, an alarm sound and a premating sound. The alarm sound, produced when the beetle is handled (and sometimes seemingly at random), consists of irregularly spaced chirps, 1–3 or so per second. The premating sound is a rapid series of short chirps lasting 0.3 to 3.6 seconds, with the chirps uttered rapidly at a regular rate. The premating



Donald J. Borror

Figure 26–2 Audiospectrographs of the stridulations of three species of weevils: A, *Conotrachelus carinifer* Casey; B, *C. naso* LeConte; C, *C. posticatus* Casey.

sounds of different sympatric species are different and are believed to act as a species-isolating mechanism.

In *Dendroctonus* (Curculionidae: Scolytinae), both sexes stridulate, and the sounds produced are of three general types: (1) simple chirps (each produced by a single movement of the stridulatory apparatus); (2) interrupted chirps (each produced by a single movement of the stridulatory apparatus, but interrupted by one or more brief moments of silence); and (3) clicks (each a single spike of sound, produced by females when alone in the bark). Stridulation occurs during stress situations (for example, when a beetle is handled), during aggression, and during courtship. The sounds made by females in the bark may have a territorial function; that is, they may limit the density of the burrows. Males emit interrupted chirps both while fighting a rival male and when attracted to the gallery of a virgin female. A female responds to male stridulation at the gallery entrance by simple chirps. The courting behavior in the gallery involves the male emitting simple chirps while the female is silent.

Little is known about auditory mechanisms in beetles. They do not have tympana, but certain chordotonal organs and sensilla are sensitive to vibration. These organs usually lie on either the legs or antennae.

Classification of the Coleoptera

Coleopterists differ with regard to the relationships of the various groups of beetles, the groups that should be given family status, and their arrangement into superfamilies. The recent publication of *American Beetles* (Arnett et al. 2001, 2002) reflects the opinions of more than 80 contributing specialists. The arrangement of suborders, superfamilies, and families followed in this book closely follows the classification presented by them. Some taxa in that classification depart radically from the traditional ones, but most are well founded and were arrived at by modern taxonomic methods. In a few instances, we chose to combine taxa for ease in using the key. Many individual authorities give family status to more groups than we do in this book.

An outline of the groups in the order Coleoptera, as they are treated in this book, is given here. Names in parentheses represent different spellings, synonyms, or other treatments of the group. Families marked with an asterisk (*) are relatively rare or are unlikely to be taken by the general collector. Most common names of families are those used in Arnett et al. (2001, 2002).

- Suborder Archostemata
  - Cupedidae (Cupesidae, Cupidae)—reticulated beetles*
  - Micromalthidae—telephone-pole beetles*
- Suborder Myxophaga
  - Microsporidae (Sphaeriidae)—minute bog beetles*
  - Hydroscaphidae (Hydrophilidae, in part)—skiff beetles*
- Suborder Adephaga
  - Rhysodidae (Rhyssodidae)—wrinkled bark beetles
  - Carabidae (including Cicindelidae, Paussidae, Tachypachidae, Omophronidae)—ground beetles and tiger beetles
  - Gyrinidae—whirligig beetles
  - Haliplidae—crawling water beetles
  - Noteridae (Dytiscidae, in part)—burrowing water beetles*
  - Amphizoidae—trout-stream beetles*
  - Dytiscidae—predaceous diving beetles
- Suborder Polyphaga
  - Series Staphyliniformia
    - Superfamily Hydrophiloidea
      - Hydrophilidae (including Hydrochidae, Spercheidae, Sphaeridiidae, and Georyssidae)—water scavenger beetles
      - Sphaeritidae—false clown beetles*
      - Histeridae (Niponiidae)—clown beetles
    - Superfamily Staphylinoidea
      - Hydraenidae (Limnebiidae; Hydrophilidae in part)—minute moss beetles*
      - Ptiliidae (Ptilidae, Trichopterigidae; including Limulodidae)—feather-winged beetles and horseshoe crab beetles
      - Agyrtidae (Silphidae, in part)—primitive carrion beetles
      - Leiodidae (Liodidae, Anisotomidae, Leptodiridae, Leptinidae, Platypsyllidae Catopidae; Silphidae, in part)—round fungus beetles, mammal-nest beetles, and beaver parasites*
      - Scydmaenidae—antlike stone beetles*
      - Silphidae (Necrophoridae)—carrion beetles
      - Staphylinidae (including Micropeplidae, Pselaphidae, Scaphidiidae, Dasyceridae, Brathinidae)—rove beetles
  - Series Scarabaeiformia
    - Superfamily Scarabaeoidea
      - Lucanidae—stag beetles
      - Passalidae—bess beetles
      - Diphyllostomatidae*
      - Ceratocanthidae (= Acanthoceridae) *
      - Glaphyridae*
      - Pleocomidae—rain beetles*
      - Geotrupidae—earth-boring dung beetles
      - Ochodaeidae*
      - Hybosoridae*
      - Glaresidae*
      - Trogidae—skin beetles
      - Scarabaeidae—scarab beetles
  - Series Elateriformia
    - Superfamily Scirtoidea
      - Eucinetidae (Dascillidae, in part)—plate-thigh beetles*
      - Clambidae—minute beetles
      - Scirtidae (Helodidae, Cyphonidae; Dascillidae, in part)—marsh beetles
    - Superfamily Dascilloidea
      - Dascillidae (Atopidae, Dascyllidae; including Karumiidae)—soft-bodied plant beetles
      - Rhipiceridae (Sandalidae, in part)—cicada parasite beetles
    - Superfamily Buprestoidea
      - Buprestidae (including Schizopodidae)—metallic wood-boring beetles
    - Superfamily Byrrhoidea
      - Byrrhidae—pill beetles
      - Elmidae (Limniidae, Helminthidae)—riffle beetles
      - Dryopidae (Parnidae)—long-toed water beetles
      - Lutrochidae—travertine beetle
      - Limnichidae (Dascillidae, in part)—minute marsh-loving beetles*
      - Heteroceridae—variegated mud-loving beetles
      - Psephenidae (including Eubriidae)—water penny beetles
      - Ptilodactylidae (Dascillidae, in part)
      - Chelonariidae*—turtle beetles
      - Eulichadidae (Dascillidae, in part) *
      - Callirhipidae (Rhipiceridae, in part, Sandalidae, in part)—cedar beetles*
    - Superfamily Elateroidea
      - Artematopodidae (Eurypogonidae; Dascillidae, in part) *
      - Brachypsectridae—the Texas beetle*
      - Cerophytidae—rare click beetles*
      - Eucnemidae (Melasidae, Perothopidae)—false click beetles

        - Throscidae (Trixagidae)
        - Elateridae (including Plastoceridae and Cebrionidae)—click beetles
        - Lycidae—net-winged beetles
        - Telegeusidae—long-lipped beetles*
        - Phengodidae—glowworm beetles*
        - Lampyridae—fireflies, lightningbugs
        - Omethidae—false firefly beetles; false soldier beetles
        - Cantharidae (Telephoridae, Chauliognathidae)—soldier beetles
- Series Bostrichiformia
    - Jacobsoniidae—Jacobson's beetles*
    - Superfamily Derodontoidea
        - Derodontidae—tooth-necked fungus beetles*
    - Superfamily Bostrichoidea
        - Nosodendridae—wounded tree beetles*
        - Dermestidae (including Thorictidae)—skin beetles
        - Bostrichidae (including Lyctidae, Psoidae, Apatidae)—branch and twig borers and powderpost beetles
        - Anobiidae (including Ptinidae and Gnostidae)—death watch and spider beetles
- Series Cucujiformia
    - Superfamily Lymexyloidea
        - Lymexylidae—ship-timber beetles
    - Superfamily Cleroidea
        - Trogossitidae (Ostomatidae, Ostomidae)—bark-gnawing beetles
        - Cleridae (Corynetidae)—checkered beetles
        - Melyridae (Malachiidae, Dasytidae)—soft-winged flower beetles
    - Superfamily Cucujoidea
        - Sphindidae—dry-fungus beetles*
        - Brachypteridae—short-winged flower beetles
        - Nitidulidae—sap-feeding beetles
        - Smicripidae—palmetto beetles
        - Monotomidae (Rhizophagidae)—root-eating beetles
        - Silvanidae
        - Passandridae—parasitic flat bark beetles
        - Cucujidae—flat bark beetles
        - Laemophloeidae—lined flat bark beetles
        - Phalacridae—shining flower beetles
        - Cryptophagidae—silken fungus beetles
        - Languriidae—lizard beetles
        - Erotylidae—pleasing fungus beetles
        - Byturidae—fruitworm beetles
        - Biphyllidae—false skin beetles
        - Bothrideridae—dry bark beetles
        - Cerylonidae—minute bark beetles
        - Endomychidae—handsome fungus beetles
        - Coccinellidae—ladybird beetles
        - Corylophidae—minute fungus beetles
        - Latridiidae—minute brown scavenger beetles
    - Superfamily Tenebrionoidea
        - Mycetophagidae—hairy fungus beetles
        - Archeocrypticidae*
        - Ciidae (Cisidae, Cioidae)—minute tree fungus beetles
        - Tetratomidae—polypore fungus beetles*
        - Melandryidae (including Synchroidae, Anaspididae, and Serropalpidae)—false darkling beetles
        - Mordellidae—tumbling flower beetles
        - Ripiphoridae (Rhipiphoridae)—wedge-shaped beetles
        - Colydiidae (including Adimeridae, Merycidae, and Monoedidae)—cylindrical bark beetles
        - Zopheridae (including Monommatidae, Monommidae)—ironclad beetles
        - Tenebrionidae (including Alleculidae and Lagriidae)—darkling beetles
        - Prostomidae—jugular-horned beetles*
        - Synchroidae
        - Oedemeridae—pollen-feeding beetles
        - Stenotrachelidae (Cephaloidae)—false long-horned beetles*
        - Meloidae—blister beetles
        - Mycteridae (including Hemipeplidae)—palm and flower beetles
        - Boridae—conifer bark beetles
        - Pythidae—dead log bark beetles
        - Pyrochroidae (including Pedilidae and Cononotidae)—fire-colored beetles
        - Salpingidae—narrow-waisted bark beetles
        - Anthicidae—antlike flower beetles
        - Aderidae (Euglenidae)—antlike leaf beetles*
        - Scraptiidae—false flower beetles
        - Polypriidae—the red cross beetle
    - Superfamily Chrysomeloidea
        - Cerambycidae (including Disteniidae, Parandridae, and Spondylidae)—long-horned beetles
        - Megalopodidae
        - Orsodacnidae
        - Chrysomelidae (including Bruchidae, Cassididae, Cryptocephalidae, Hispidae, and Sagridae)—leaf beetles
    - Superfamily Curculionoidea (Rhynchophora)
        - Nemonychidae (Cimberidae)—pine flower snout beetles

Anthribidae (Platystomidae, Bruchelidae, Choragidae, Platyrrhinidae)—fungus weevils
Belidae—primitive weevils
Attelabidae (Rhynchitidae)—tooth-nosed snout beetles; leaf-rolling weevils
Brentidae (Brenthidae, including Apionidae and Cyladidae)—straight-snouted weevils and pear-shaped weevils
Ithyceridae—the New York weevil
Curculionidae (including Cossonidae, Rhynchophoridae, Platypodidae, and Scolytidae)—snout beetles, true weevils, and bark beetles

Characters Used in Identifying Beetles

The principal characters of beetles used in identification are those of the head, antennae, thoracic sclerites, legs, elytra, and abdomen. Occasionally characters such as size, shape, and color are used. In most cases the ease of recognizing these characters depends on the size of the beetle. Some characters require careful observation, often at high magnification, for accurate interpretation.

Head Characters

The principal head character used involves the development of a snout. In the Curculionoidea, the head is more or less prolonged forward into a snout; the mouthparts are reduced in size and are located at the tip of the snout; and the antennae usually arise on the sides of it. The basal antennal segment, the scape, often fits into a groove (the *scrobe*; Figure 26–3, *agr*) on the snout. In many cases (Figure 26–3), the snout is quite distinct, occasionally as long as the body or longer. In other cases (for example, the Scolytinae and Platypodinae), the snout is poorly developed and not very evident as such. The families in the Curculionoidea are sometimes placed in a separate group, the Rhynchophora. These beetles differ from most other members of the order in having fused gular sutures (Figure 26–3C). There is some development of a snout in a few beetles outside this superfamily, but such beetles have separated gular sutures (Figure 26–4, *gs*).

Antennae

The antenna of the Coleoptera consists of only three true segments, that is, subdivisions characterized by intrinsic musculature. The basal segment is the scape, followed by the pedicel and the flagellum. In most insects, the flagellum is then divided into unmusculated subsegments, sometimes quite a lot. Entomologists traditionally have recognized that these subsegments differ from the three true segments of the antenna, but nevertheless have called them all "antennal segments." The subdivisions of the flagellum more properly should be called *flagellomeres*. In this chapter we avoid the term "antennal segment" and refer to them as *antennomeres*.

The antennae of beetles are subject to considerable variation in different groups, and these differences are used in identification. The term *clubbed,* as used in the key, refers to any condition in which the terminal antennomeres are larger than those preceding them, including *clavate* (the terminal antennomeres enlarging gradually and only slightly, as in Figure 2–15D,E); *capitate* (the terminal antennomeres abruptly enlarged, as in Figure 26–5F–I); *lamellate* (the terminal antennomeres expanded on one side into rounded or oval plates, as in Figure 26–6A,C–G); and *flabellate* (the terminal antennomeres expanded on one side into long, thin, parallel-sided, tonguelike processes, as in Figure 26–6B). The distinction between some of these

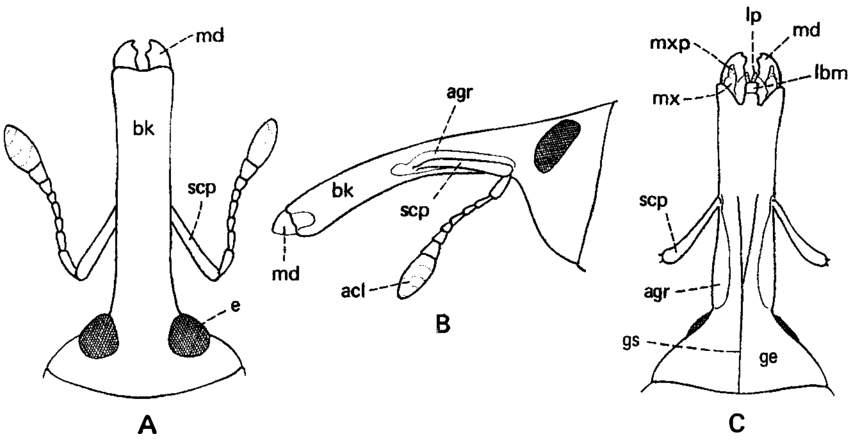


Figure 26–3 Head of a snout beetle (*Pissodes*, Curculionidae). A, dorsal view; B, lateral view; C, ventral view. *acl*, antennal club; *agr*, scrobe, groove in beak for reception of antenna; *bk*, beak or snout; *e*, compound eye; *ge*, gena; *gs*, gular suture; *lbm*, labium; *lp*, labial palp; *md*, mandible; *mx*, maxilla; *mxp*, maxillary palp; *scp*, scape of antenna.

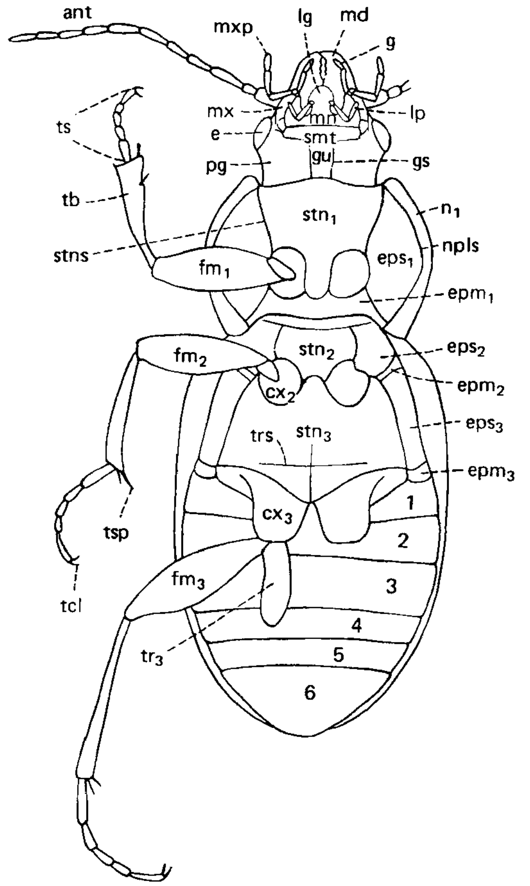


Figure 26–4 Ventral view of a ground beetle (*Omaseus* sp.). *ant*, antenna; *cx*, coxa; *e*, compound eye; epm_1, proepimeron; epm_2, mesepimeron; epm_3, metepimeron; eps_1, proepisternum; eps_2, mesepisternum; eps_3, metepisternum; *fm*, femur; *g*, galea; *gs*, gular suture; *gu*, gula; *lg*, ligula; *lp*, labial palp; *md*, mandible; *mn*, mentum; *mx*, maxilla; *mxp*, maxillary palp; n_1, pronotum; *npls*, notopleural suture; *pg*, postgena; *smt*, submentum; stn_1, prosternum; stn_2, mesosternum; stn_3, metasternum; *stns*, prosternal suture; *tb*, tibia; *tcl*, tarsal claws; *tr*, trochanter; *trs*, transverse suture on metasternum; *ts*, tarsus; *tsp*, tibial spurs; *1–6*, ventrites 1–6.

antennal variations (for example, between filiform and slightly clubbed or between filiform and serrate) is not very sharp, and some conditions might be interpreted in different ways. This fact is taken into account in the key, as specimens will key out correctly from either alternative at many places in the key.

The number of terminal antennomeres that form the club (in clubbed antennae) often serves as a key character. The antennomeres between the scape (the basal segment) and the club are sometimes referred to as the *funiculus* (or *funicle*).

Thoracic Characters

The pronotum and scutellum are normally the only thoracic areas visible from above. The other thoracic areas are usually visible only in a ventral view. Viewed from above, the pronotum may vary greatly in shape, and its posterior margin may be convex, straight, or sinuate (Figure 26–7E–G). Laterally, the pronotum may be margined (with a sharp, keel-like lateral edge) or rounded. The surface of the pronotum may be bare or pubescent, and it may be smooth or with various punctures or dents, ridges, grooves, tubercles, or other features. The underside of the pronotum is called the hypomeron. The scutellum (the mesoscutellum) is usually visible as a small, triangular sclerite immediately behind the pronotum, between the bases of the elytra. Only occasionally is it rounded or heart-shaped, and sometimes it is concealed.

The chief thoracic characters apparent in a ventral view that are important in identification are the various sutures, the shape of certain sclerites, and the particular sclerites adjacent to the front and middle coxae. A few beetles (the Adephaga, Myxophaga, and Cupedidae) have notopleural sutures (Figure 26–4, *npls*), which separate the pronotum from the propleura. Most beetles have prosternal sutures (Figure 26–4, *stns*), which separate the prosternum from the rest of the prothorax. The anterior margin of the prosternum is usually straight. When it is somewhat convex (as in Figure 26–8A), it is said to be lobed. The prosternum often has a process or lobe extending backward between the front coxae, and sometimes (for example, in click beetles, Figure 26–8A) this process is spinelike.

When the sclerites of the prothorax extend posteriorly around the front coxae, these coxal cavities are said to be closed (Figure 26–7B). When the sclerite immediately behind the front coxae is a sclerite of the mesothorax, these cavities are said to be open (Figure 26–7A). When the middle coxae are surrounded by sterna and are not touched by any pleural sclerite, these coxal cavities are said to be closed (Figure 26–7D). When at least some of the pleural sclerites reach the middle coxae, these coxal cavities are said to be open (Figure 26–7C).

The “click mechanism” consists of a long prosternal intercoxal process with the dorsal or dorsoapical surface of the apex notched to fit against a slight projection on the anterior margin of the relatively large, deep midcoxal cavity. In some compact species, there is a platelike, margined ventral face to the postcoxal portion of the intercoxal process that is tightly received by

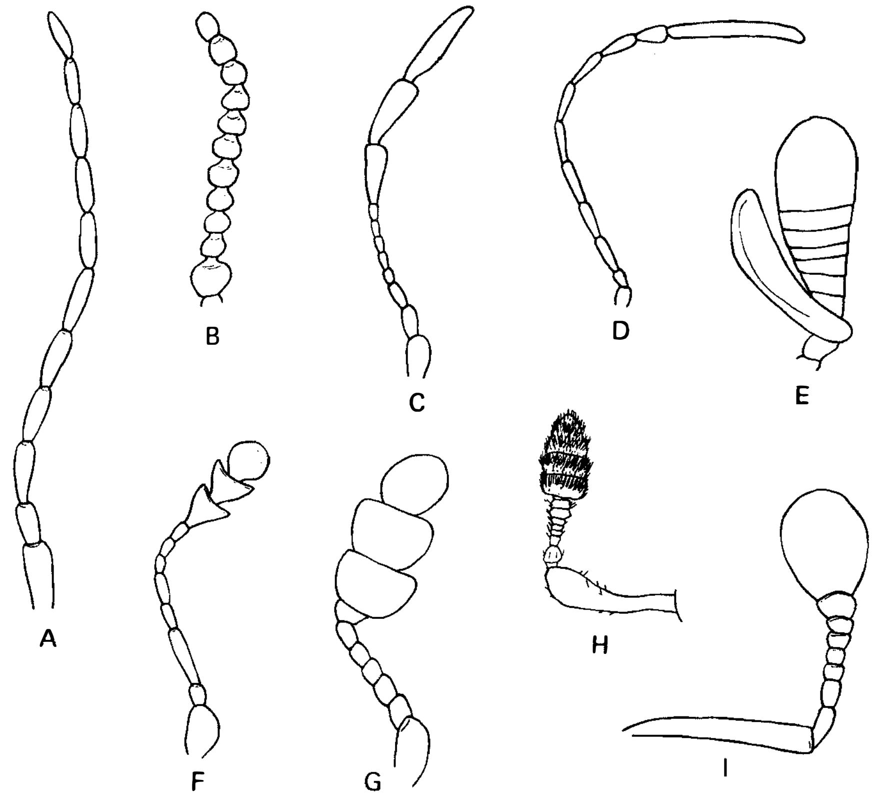


Figure 26–5 Antennae of Coleoptera. A, *Harpalus* (Carabidae); B, *Rhysodes* (Rhysodidae); C, *Trichodesma* (Anobiidae); D, *Arthromacra* (Tenebrionidae); E, *Dineutus* (Gyrinidae); F, *Lobiopa* (Nitidulidae); G, *Dermestes* (Dermestidae); H, *Hylurgopinus* (Curculionidae); I, *Hololepta* (Histeridae). (H, redrawn from Kaston.)

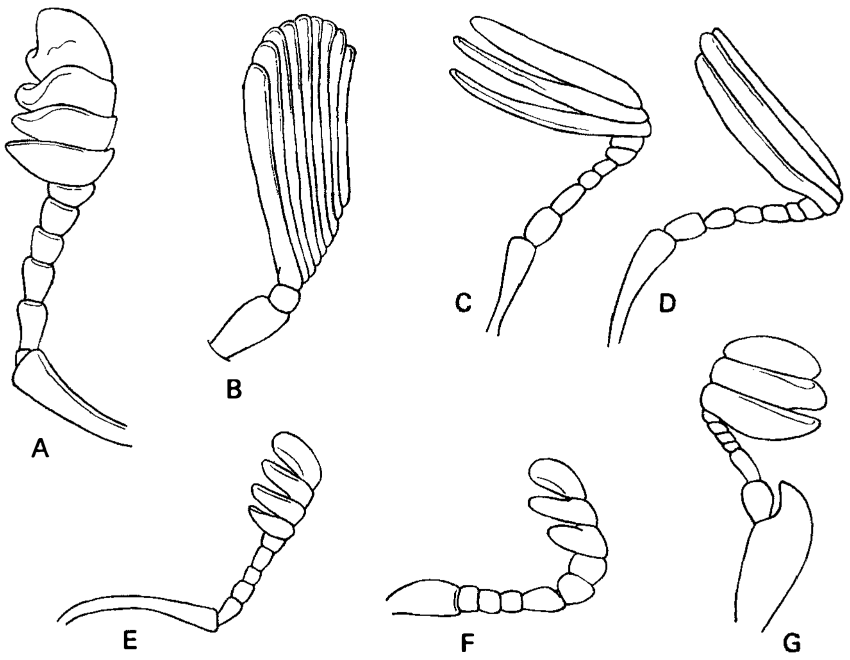


Figure 26–6 Antennae of Coleoptera. A, *Nicrophorus* (Silphidae); B, *Sandalus*, male (Rhipiceridae); C, *Phyllophaga*, (Scarabaeidae), the terminal segments expanded; D, same, terminal segments together forming a club; E, *Lucanus* (Lucanidae); F, *Odontotaenius* (Passalidae); G, *Trox* (Trogidae).

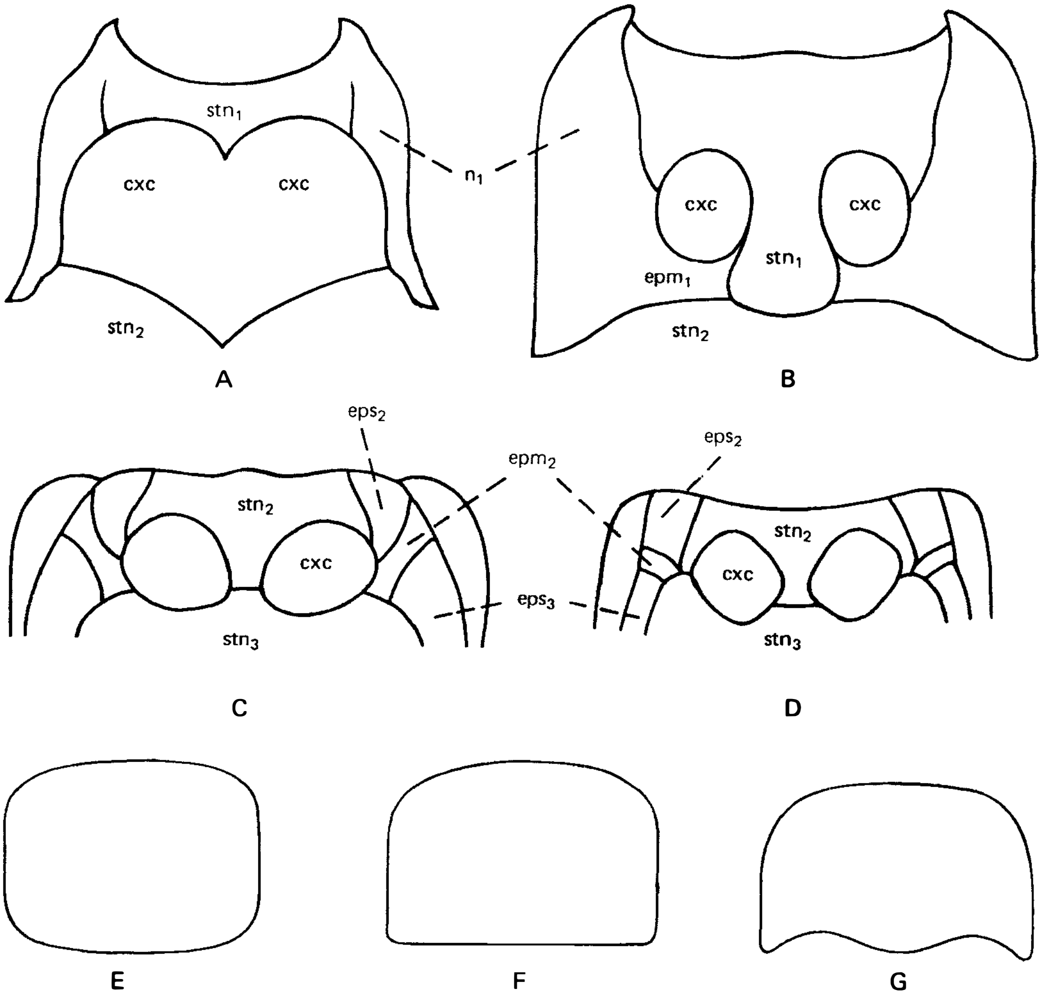


Figure 26–7 Thoracic structure in Coleoptera. A and B, prosterna showing open (A) and closed (B) coxal cavities; C and D, mesosterna showing open (C) and closed (D) coxal cavities; E–G, pronota with posterior margin convex (E), straight (F), or sinuate (G). *cxc*, coxal cavity; epm_1, proepimeron; epm_2, mesepimeron; eps_2, mesepisternum; eps_3, metepisternum; stn_1, prosternum; stn_2, mesoternum; stn_3, metasternum.

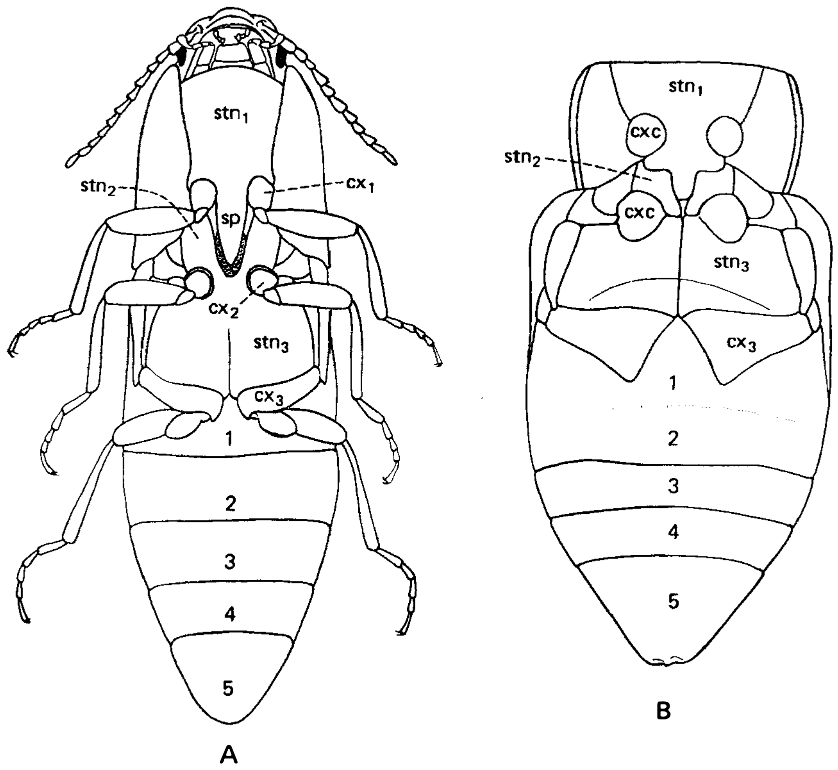


Figure 26–8 A, ventral view of a click beetle (*Agriotes*); B, ventral view of the thorax and abdomen of a metallic wood-boring beetle (*Chrysobothris*). *cx*, coxa; *cxc*, coxal cavity; *sp*, prosternal spine; *stn*$_1$, prosternum; *stn*$_2$, mesosternum; *stn*$_3$, metasternum; *1–5*, ventrites 1–5.

the deeply emarginate mesosternum. In these cases, the true apex of the prosternum is hidden in a deep cavity between the mid coxae.

Leg Characters

The coxae of beetles vary greatly in size and shape. In some cases they are globose or rounded and project only slightly. When they are more or less elongate laterally without projecting very much, they are said to be *transverse*. Sometimes they are more or less conical and noticeably project ventrad. A distinct posterior face on the hind coxa can be seen by viewing the specimen from the side. A few beetles have a small sclerite, the trochantin, in the anterolateral portion of the coxal cavity (Figure 26–9B, *tn*).

When disturbed, many beetles draw their appendages in close to the body and "play dead." Such beetles often have grooves in the body or in certain leg segments into which the appendages fit when so retracted. Beetles with retractile legs usually have grooves in the coxae (particularly the middle or hind coxae) into which the femora fit when the legs are retracted, and they may have grooves in other leg segments.

The tarsal segment of beetles is divided into unmusculated units. As in the antenna, these subdivisions are often referred to as "segments," but are more accurately called *tarsomeres*. The number and relative size and shape of the tarsomeres are very important characters for identifying beetles. It is necessary to examine the tarsi of almost any beetle one wishes to run through the key. The number of tarsomeres in most beetles varies from three to five. It is usually the same on all tarsi, but some groups have one less tarsomere in the hind tarsi than in the middle and front tarsi, and others have fewer tarsomeres in the front tarsi. The tarsal formula is an important part of any group description and is given as 5-5-5, 5-5-4, 4-4-4, 3-3-3, and so on, indicating the number of tarsomeres on the front, middle, and hind tarsi, respectively. Most Coleoptera have a 5-5-5 tarsal formula.

In a few groups, including some very common beetles, the next to the last tarsomere is very small and inconspicuous. Such a tarsomere may be very difficult to see unless very carefully examined under high magnification. These tarsi thus seem to have one tarsomere less than they actually have, and are so described in the key. For example, a five-merous tarsus such as the one shown in Figure 26–10A is described in the key as "apparently four-merous." A few groups have the basal tarsomere very small (Figure 26–10D) and visible only if the tarsus is properly oriented. If the tarsi of a beetle

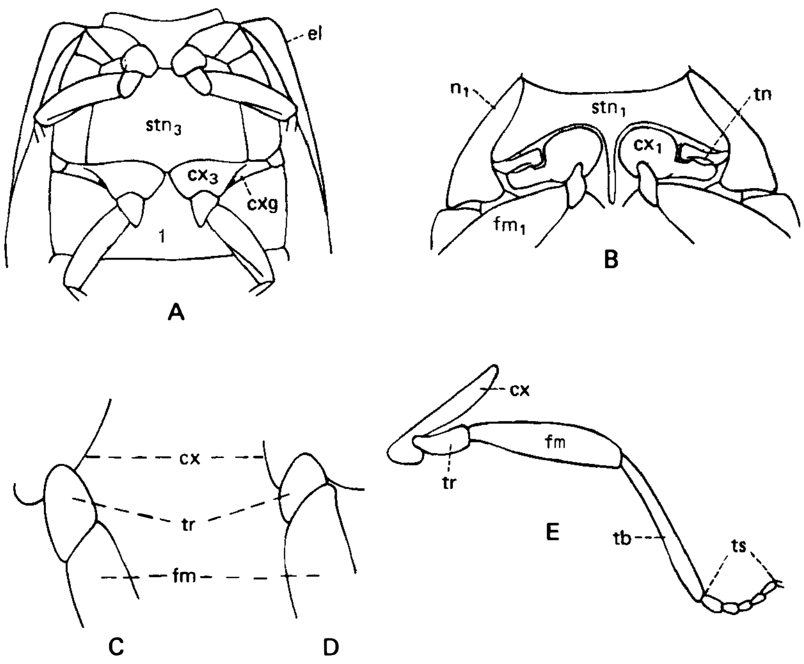


Figure 26–9 Leg structure in Coleoptera. A, thorax of *Dermestes* (Dermestidae), ventral view, showing grooved hind coxae; B, prothorax of *Psephenus* (Psephenidae), ventral view, showing trochantin; C, base of hind leg of *Apion* (Brentidae); D, base of hind leg of *Conotrachelus* (Curculionidae); E, hind leg of *Trichodesma* (Anobiidae), showing interstitial trochanter. *cx*, coxa; *cxg*, groove in coxa; *el*, elytron; *fm*, femur; n_1, pronotum; stn_1, prosternum; stn_3, metasternum; *tb*, tibia; *tn*, trochantin; *tr*, trochanter; *ts*, tarsus; *1*, first ventrite.

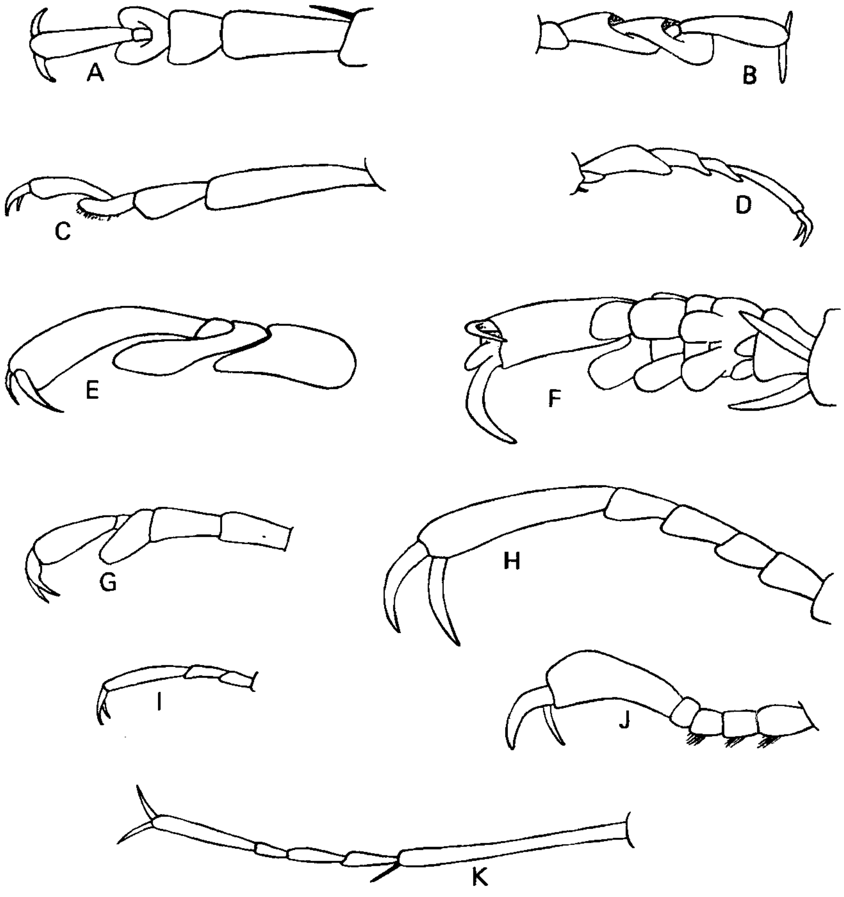


Figure 26–10 Tarsi of Coleoptera. A, *Megacyllene*, (Cerambycidae); B, *Necrobia* (Cleridae); C, *Nacerda* (Oedemeridae), hind leg; D, *Trichodes* (Cleridae); E, *Chilocorus* (Coccinellidae); F, *Sandalus* (Rhipiceridae); G, *Scolytus* (Curculionidae); H, *Psephenus* (Psephenidae); I, a latridiid; J, *Parandra* (Cerambycidae); *Platypus* (Curculionidae).

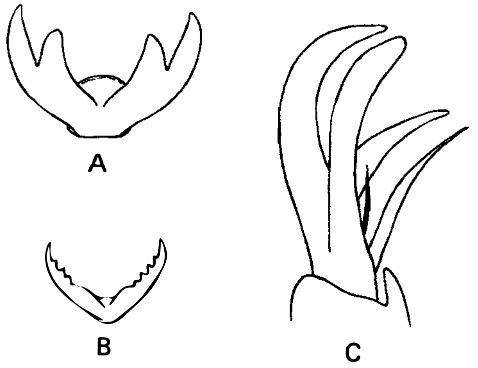


Figure 26–11 Tarsal claws of Coleoptera. A, toothed (Coccinellidae); B, pectinate (Tenebrionidae: Alleculinae); C, cleft (Meloidae).

appear to be four-merous and the third tarsomere is relatively large and more or less U-shaped (Figure 26–10A), they are generally five-merous, with the fourth tarsomere very small. If the tarsi appear to be four-merous and the third tarsomere is slender and not greatly different from the terminal tarsomere, then they either are actually four-merous or are five-merous with the basal tarsomere very small.

The pretarsal claws of beetles vary somewhat. In most cases they are simple, that is, without branches or teeth, but in some cases they are toothed, pectinate, or cleft (Figure 26–11).

The Elytra

The elytra normally meet in a straight line down the middle of the body. This line of union of the elytra is called the *suture*. The suture may extend to the tips of the elytra, or the tips may be slightly separated. The anterolateral angles of the elytra are called the *humeri*. The elytra usually slope gradually from the suture to the outer edge. When they are abruptly bent down laterally, the bent-down portion is called the *epipleura* (plural, *epipleurae*).

The elytra vary mainly in shape, length, and texture. They are usually parallel-sided anteriorly and tapering posteriorly. Sometimes they are more or less oval or hemispherical. The elytra of some beetles are truncate at the apex. The elytra in some groups are variously sculptured, with ridges, grooves or striae, punctures, tubercles, and the like. In other cases they are quite smooth. If the elytra appear hairy under low or medium magnification, they are said to be *pubescent*. The elytra of some beetles are quite hard and stiff, and curve around the sides of the abdomen to some extent. In others they are soft and pliable and lie loosely on top of the abdomen without firmly embracing it.

The Abdomen

The structure of the first abdominal segment differentiates the two principal suborders of the Coleoptera. In the Adephaga the hind coxae extend backward and bisect the first abdominal sternum so that, instead of extending completely across the body, this sternum is divided and consists of two lateral pieces separated by the hind coxae (Figures 26–4 and 26–12A). In the Polyphaga the hind coxae extend backward a different distance in different groups, but the first abdominal sternum is never completely divided, and its posterior edge extends completely across the body.

The beetle abdomen often has one or two basal segments highly reduced and visible only by dissection. Coleopterists call the remaining visible abdominal sterna *ventrites*, and the numbering begins from the base, with ventrite 1 appearing adjacent to the metathorax. The number of ventrites varies in different

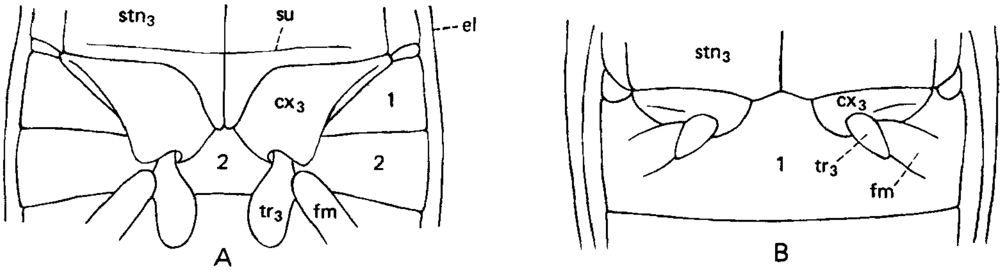


Figure 26–12 Base of abdomen, ventral view, showing difference between Adephaga and Polyphaga. A, tiger beetle (Adephaga); B, pleasing fungus beetle (Polyphaga). cx_3, hind coxa; *el*, elytron; *fm*, hind femur; stn_3, metasternum; *su*, transverse metasternal suture; tr_3, hind trochanter; *1, 2*, ventrites 1, 2.

groups and is repeatedly used in the key. In a few cases (for example, the Buprestidae), the first two visible sterna are more or less fused together, and the suture between them is much less distinct than the other abdominal sutures, the connate condition (Figure 26–8B). This condition can often be detected by (1) a difference in the appearance of the suture between those ventrites that are connate and those that are not; (2) the absence of a membrane between the ventrites; or (3) by a reduction in the depth of the suture itself, especially medially. The easiest and most certain way to tell is to view the upturned lateral portion of the ventrite that is held against the elytron. Connate ventrites are obviously immobile in this view, and they lack the hinged form of the free, movable state. If the sutures between the abdominal sterna are all equally distinct, then no segments are said to be fused.

The last abdominal tergum, often called the *pygidium,* is sometimes exposed beyond the tips of the elytra.

Other Characters

Characters such as size, shape, or color should not prove particularly difficult. The term *base* is used to distinguish the two ends of body parts. When speaking of an appendage, the base is the end nearest the body. The base of the head or pronotum is the posterior end, and the base of the elytra or abdomen is the anterior end. The subdivisions of the tarsi (tarsomeres) or antennae (antennomeres) are numbered from the base distad.

Key to the Families of Coleoptera

The phylogeny and classification of beetles is an area of intense research interest, and there have been a number of changes since the last edition of this book. The following key is largely the generous contribution of Dr. Michael A. Ivie (Montana State University), whose assistance is gratefully acknowledged. The key is rather long, not only because this is the largest order of insects, but also because there is quite a bit of variation in many families. The key is constructed to take this variation into account and also to provide for specimens whose characters are somewhat borderline. Many specimens key out correctly from either alternative at certain points in the key. Groups marked with an asterisk (*) are relatively rare or are not very likely to be taken by the general collector. This key is to adults. Keys to larvae are given by Lawrence et al. (1991).

1.	Elytra present, complete, short, or reduced to flaplike stubs on the mesothorax	2	
1′.	Elytra totally absent	193	
2(1).	Notopleural sutures present (Figure 26–4, npls)	3	
2′.	Notopleural sutures absent	12	
3(2).	Hind coxa immovably fused to metasternum, completely dividing first ventrite (Figures 26–4, 26–12A); elytra smooth with scattered punctures, microsculptured, simply punctate or striate; body rarely with scales (Adephaga)	4	
3′.	Hind coxa free, first ventrite extending entirely across venter behind them (Figures 26–8, 26–12B)	10	
4(3).	Hind coxa greatly enlarged, a ventral plate concealing trochanter and basal half of femur, covering most of 3 basal ventrites (Figure 26–19B)	Haliplidae	p. 405
4′.	Hind coxa greatly enlarged or not, if hind coxa greatly enlarged, then all ventrites visible laterally, coxa not concealing trochanter, basal half of femur or first 3 ventrites (Figures 26–4, 26–17)	5	
5(4′).	Fore tibia with antenna cleaner on inner apical angle; head with supraorbital setae	6	
5′.	Fore tibia without antenna cleaner on inner apical angle; head lacking supraorbital setae	7	

6(5).	Mentum expanded, fused laterally to head capsule, covering ventral mouthparts completely when mandibles closed, mentum extending anteriorly beyond other mouthparts to form cutting edge; outer angle of fore tibia with large, inwardly curved uncus; body cylindrical; antenna moniliform; head, pronotum and elytra with deep canaliculate grooves	Rhysodidae	p. 401
6′.	Mentum not fused laterally to head capsule or extending beyond other mouthparts, maxilla and labium with at least palpi visible (Figure 26–4); outer angle of fore tibia with straight or outwardly curved teeth or spines (Figure 26–4); head, pronotum, and elytra without deep canaliculate grooves; body form and antenna variable	Carabidae	p. 401
7(5′).	Pedicel of antenna greatly enlarged, offset from main line of antenna, flagellum very short and compact, not extended beyond hind margin of head (Figure 26–5E); mid and hind legs very short (Figure 26–17B); eyes usually divided into 2 isolated parts on each side (Figure 26–17C), rarely with only a very narrow procoss (the canthus) extending between upper and lower portions	Gyrinidae	p. 403
7′.	Pedicel of antenna normal, antenna extended beyond hind margin of head; mid and hind legs not especially short; eyes not divided	8	
8(7′).	Hind femur and tibia narrow and subcylindrical in cross section; hind tarsus shorter than tibia and not tapered distally; body not streamlined, outline of thorax and elytron discontinuous, base of pronotum distinctly narrower than elytra; length 11–16 mm	Amphizoidae	p. 405
8′.	Hind femur and tibia more or less distinctly compressed, especially in larger species (length ≥6 mm); hind tarsus usually as long or longer than tibia, distinctly tapering distally; body streamlined, outline of pronotum and elytron usually conjointly rounded (Figures 26–20A,C); length 1–40 mm	9	
9(8′).	Body 1.0–5.0 mm long; fore tarsus with 5 distinct tarsomeres; eyes usually normally developed	Noteridae	p. 405
9′.	Body usually >6 mm long, if smaller, then scutellum visible, or fore tarsus pseudotetramerous, or compound eyes absent or greatly reduced in size and indistinct	Dytiscidae	p. 405
10(3′)	Elytra reticulate with rows of square punctures; body covered in scales; length >5 mm	Cupedidae	p. 401
10′.	Elytra glabrous; length <2 mm	11	
11(10′)	Body hemispherical; elytra covering all abdominal terga; abdomen with 3 ventrites; antenna with 11 antennomeres, 9–11 forming club	Microsporidae	p. 401
11′.	Body more elongate-oval and depressed dorsoventrally; elytra short, 3–4 abdominal tergites exposed; abdomen with 6–7 ventrites; antenna with 9 antennomeres, antennomere 9 forming narrow club	Hydroscaphidae	p. 401
12(2′).	Antenna with strongly asymmetrical, usually lamellate club of 3–8 antennomeres (Figures 26–6C–G); fore coxa large, strongly transverse or conical and projecting below prosternum; fore coxal cavity closed; trochantin concealed (except in Diphyllostomatidae); fore tibia flattened, with 1 or more teeth on outer edge; tarsi with 5 distinct tarsomeres, none of which are lobed or densely pubescent	13	
12′.	Antenna not lamellate, or coxa, tibia, or tarsi not as in preceding entry	24	
13(12).	Antenna with 11 antennomeres	14	
13′.	Antenna with fewer than 11 antennomeres	15	

14(13).	Antennal club with 4–7 elongate antennomeres	Pleocomidae	p. 411
14′.	Antennal club with 3 circular or oval antennomeres	Geotrupidae	p. 412
15(13′).	Body capable of being rolled into contractile ball; middle and posterior tibiae flattened and dilated	Ceratocanthidae	p. 411
15′.	Body oblong, not capable of being rolled into ball; middle and posterior tibiae not significantly flattened and dilated	16	
16(15′).	Longer apical spur of mid tibia pectinate along one edge	Ochodaeidae	p. 412
16′.	Longer apical spur of mid tibia simple, not pectinate	17	
17(16′).	Antennomeres of antennal club not capable of being tightly closed together (Figures 26–6E–F)	18	
17′.	Antennomeres of antennal club capable of being closed together (Figures 26–6C,D,G)	20	
18(17).	Abdomen with 7 ventrites, the first divided by hind coxa; head strongly constricted behind eyes; fore tibia lacking apical spurs; trochantin exposed; mid coxa conical and projecting; length 5–9 mm	Diphyllostomatidae	p. 411
18′.	Abdomen with 5–6 ventrites, the first not divided; head not strongly constricted behind eyes; fore tibia with 1 or 2 apical spurs; trochantin not visible; mid coxa not projecting; length 8–60 mm	19	
19(18′).	Mentum with apex deeply emarginate (Figure 26–13A); mid coxal cavity closed laterally; body distinctly flattened dorsally (Figure 26–28C)	Passalidae	p. 411
19′.	Mentum with apex simple, not deeply emarginate (Figure 26–13D); midcoxal cavity open laterally; body evenly convex dorsally (Figures 26–28A,B)	Lucanidae	p. 411
20(17′).	Antennal club with 3 antennomeres, first hollowed out to receive second	Hybosoridae	p. 412
20′.	Antennal club with 3–7 antennomeres, first simple, not hollowed out to receive second (for example, see Figure 26–6C)	21	
21(20′).	Abdomen with 5 ventrites; dorsal surface roughened or tuberculate, not shining (Figure 26–29)	22	
21′.	Abdomen with 6 ventrites; dorsal surface variably sculptured, shining or not	23	
22(21).	Eyes not divided by canthus; clypeus with sides narrowing apically; color brown, gray, or black; hind femur and tibia not enlarged, not covering abdomen (Figure 26–29B)	Trogidae	p. 412
22′.	Eyes divided by prominent canthus; clypeus with sides subparallel to divergent anteriorly; color testaceous to light reddish brown; hind femur and tibia enlarged, covering most of abdomen	Glaresidae	p. 412
23(21′).	Elytra shortened and widely divergent at apex (except in *Lichnanthe lupina*), not covering pygidium; eighth morphological abdominal segment with spiracle	Glaphyridae	p. 411
23′.	Elytra not shortened or widely divergent at apex, pygidium exposed or not (Figures 26–29C,D, 26–30, 26–32, 26–33, 26–34); eighth morphological abdominal segment lacking spiracle	Scarabaeidae	p. 412
24(12′).	Hind tarsus with 2–5 tarsomeres, but never pseudotetramerous (third of 5 tarsomeres on hind leg not lobed beneath and enclosing small fourth, any other configuration possible) (Figures 26–10C–F,H–K)	25	
24′.	Hind tarsus pseudotetramerous, with apparent penultimate tarsomere lobed below, enclosing and nearly hiding true fourth tarsomere (Figures 26–10A–B,G, 26–87G–I)	26	

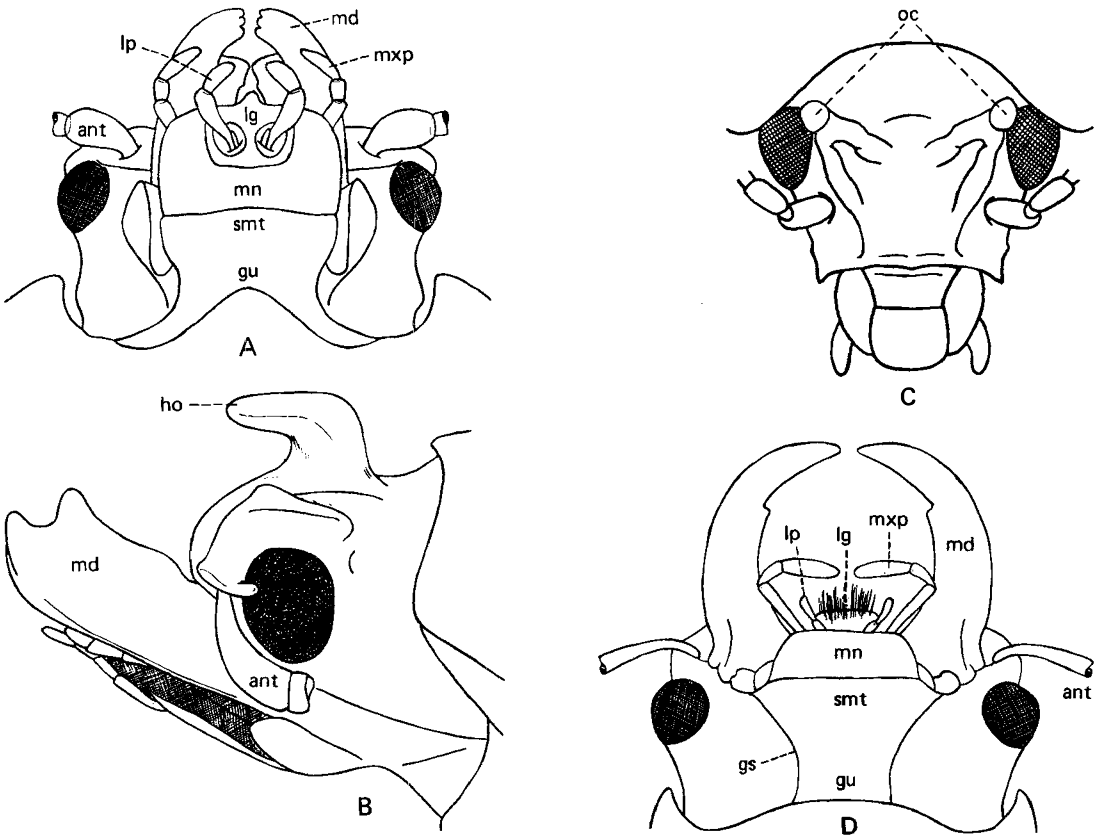


Figure 26–13 Heads of Coleoptera. A, ventral view, and B, lateral view, of *Odontotaenius disjunctus* (Illiger) (Passalidae); C, *Derodontus* (Derodontidae); D, *Pseudolucanus* (Lucanidae). *ant*, base of antenna; *gs*, gular suture; *gu*, gula; *ho*, horn; *lg*, ligula; *lp*, labial palp; *md*, mandible; *mn*, mentum; *mxp*, maxillary palp; *oc*, ocelli; *smt*, submentum.

25(24). Palps very short, usually immovably fixed and not visible; either head rostrate, prolonged into a beak (Figure 26–84A) or antenna geniculate with compact club (Figure 26–94A–C) 27

25′. Palps longer, flexible, and usually evident (for example, see Figure 26–4); head usually not prolonged into a beak but if rostrate or antenna elbowed and club compact, then palps longer and flexible 38

26(24′). Hind coxa without exposed posterior face; antenna never straight and clubbed; often with one of the following: antenna long and simple (Figures 26–73, 26–74), antenna geniculate and clubbed, head rostrate (Figures 26–87A,C), or hind femur enlarged 27

26′. Either hind coxa with distinct posterior face (at least medially) set off from ventral surface by a carina or flange, or antenna strongly or weakly clubbed but not geniculate and head not at all rostrate 77

27 (25,26).	Antenna usually without distinct club, either filiform, moniliform, serrate or pectinate (Figures 26–5A–B); head not rostrate; if antenna distinctly clubbed, then club with 5 or more antennomeres, length of head from vertex to clypeal margin ≤ to width of head just behind eyes	28	
27′.	Antenna with distinct club with 4 or fewer antennomeres (Figures 26–5H, 26–84B, 26–85A–D, 26–87A–G); or if antenna moniliform (Figure 26–5B), then head distinctly rostrate (Figure 26–84A); or if club composed of 5 or more antennomeres, then length of head from vertex to clypeal margin > width of head just behind eyes	32	
28(27).	Prosternum in front of fore coxae longer than intercoxal process; body length <5 mm; mandible with dorsal setose cavity, covered by clypeus when closed; with or without dorsobasal tubercle that fits into side of clypeus; dorsally flattened; elytra covered with fine, moderately dense, suberect to erect setae (Psammoecini)	Silvanidae	p. 431
28′.	Prosternum usually shorter than or subequal in length to intercoxal process; if longer, then body length >7 mm; mandible lacking dorsal setose cavity and dorsobasal tubercle; body form and setation variable	29	
29(28′).	Antenna usually longer than one half length of body, often inserted on prominence, capable of being reflexed backward over body (Figures 26–73, 26–74); tibiae with 2 obvious apical spurs; first antennomere usually several times longer that second; pygidium never sclerotized and exposed; length 3–75 mm in North America	Cerambycidae	p. 441
29′.	Antenna usually less than half length of body, seldom inserted on prominence, not reflexed back over body; tibiae with 0–2 apical spurs; length of first antennomere seldom more than 2–3 times length of second; pygidium of some species sclerotized and exposed; length usually <12 mm in North America	30	
30(29′).	All tibiae with 2 distinct apical spurs; front without X-shaped grooves; mesonotum with or without stridulatory file; ligula large, membranous, bilobed; aedeagus with median struts and tegmen bilobed	31	
30′.	Either at least 1 tibia fewer than 2 apical spurs or front with deep X-shaped grooves; mesonotum without stridulatory file; ligula normal; aedeagus without median struts	Chrysomelidae	p. 445
31(30).	Head with short but distinct temple behind eye, set off from narrowed neck; apex of mandible bidentate; ligula with a single lobe; mesonotum with stridulatory file	Megalopodidae	p. 445
31′.	Head lacking temples, evenly narrowed from behind eyes to neck; apex of mandible unidentate or bidentate; ligula bilobed; mesonotum without stridulatory file	Orsodacnidae	p. 445
32(27′).	Antenna geniculate (rarely appearing straight or nearly so), club compact (Figures 26–87A, 26–94); hind trochanter not cylindrical, femur attached obliquely	Curculionidae	p. 453
32′.	Antenna straight, club loose or not evident; if antenna geniculate (very rare), hind trochanter cylindrical and squarely attached to femur	33	
33(32′).	Labrum visible and free; second tarsomere not spongy beneath; maxillary palpi normal	34	
33′.	Labrum never free; tarsi variable; maxillary palpi rigid	35	
34(33).	Antenna situated adjacent to eye or laterally near base of short dorsoventrally flat rostrum; apex of third antennomere reaching well beyond front margin of eye; all tibiae lacking spurs or spurs vestigial; notosternal sutures indistinct to obsolete	Anthribidae	p. 451

34'.	Antenna situated distally on long, cylindrical rostrum; apex of third antennomere not or barely reaching front margin of eye; all tibiae with spurs; notosternal sutures distinct	Nemonychidae	p. 451
35(33').	Either with antenna moniliform and body elongate (Figure 26–84A) (Brentinae, Cyphagoginae, Trachelizinae); or antenna straight and clubbed, body pear-shaped, hind trochanter cylindrical, squarely joined to femur (Apioninae, Nanophyinae); or antenna geniculate, body pear-shaped and hind trochanter cylindrical, squarely joined to femur (Nanophyinae); or antenna with 9–10 antennomeres and body elongate-cylindrical (Figure 26–86) (Cyladinae, Nanophyinae)	Brentidae	p. 453
35'.	Antenna straight, not geniculate, with 11 antennomeres, club distinct (Figures 26–85C–D); hind trochanter triangular or diamond-shaped, obliquely joined to femur; body form variable	36	
36(35').	Gena produced anteriorly on each side, visible in frontal view as large tooth on each side of apex of rostrum, laterad of mandible; dorsal surface with obvious, recumbent, scalelike setae; body surface lacking metallic sheen; length 12 mm or more	Ithyceridae	p. 453
36'.	Gena not produced anteriorly; upper surface glabrous or with fine, hairlike setae; body surface often with distinct metallic sheen; length variable, mostly <10 mm	37	
37(36').	Antenna separated from eye by distance at least equal to width of first antennomere, positioned laterally on long quadrate rostrum (Figure 26–85H) or very close to eye at base of short, robust rostrum; fore tibia with anterior face apically flat, simple, not distinct from rest of surface; hind femur with dorsal margin slightly to moderately arched; pygidium oblique to vertical; elytron often with a scutellary striole; body surface often with distinct metallic sheen	Attelabidae	p. 451
37'.	Antenna situated immediately in front of eye at base of long, cylindrical rostrum; fore tibia with front face with shallow, grooved apical area filled with short, fine pilosity; hind femur with dorsal margin markedly arched, paddlelike in shape, femur almost as wide as long; pygidium nearly horizontal; elytron lacking scutellary striole; body surface lacking metallic sheen	Belidae	p. 451
38(25').	Length ≤1.2 mm; antenna long, thin, with loose to indistinct club; antennomeres each with a whorl of long setae at apex; wing fringed with long setae that are longer than width of wing or wing absent	Ptiliidae	p. 408
38'.	Length variable, antenna not as in preceding entry, wings rarely with fringe longer than width of wing	39	
39(38').	Head with paired ocelli (Figure 26–13C)	40	
39'.	Head without paired ocelli (a single median ocellus may be present)	42	
40(39).	Anterior edge of scutellum abruptly and sharply elevated above mesoscutum; metepisternum reaching mid coxal cavity and contacting first ventrite to separate hind coxa from edge of elytron	Derodontidae	p. 424
40'.	Anterior edge of scutellum not abruptly elevated, continuous with mesoscutum; metepisternum variable	41	
41(40').	Elytra completely covering abdomen; antenna short, not reaching middle of pronotum, with 9 antennomeres, club composed of 5 pubescent antennomeres; ventral surface with very short, dense pubescence (Ochthebiinae)	Hydraenidae	p. 408

41′.	One or more abdominal terga usually exposed beyond elytra; antenna short to long, reaching beyond middle of pronotum in those species with long elytra; antennal club, if present, not involving 5 antennomeres; underside of body without short, dense pubscence (Omaliinae)	Staphylinidae	p. 409
42(39′).	Elytra very short, leaving 3 or more abdominal tergites exposed (Figures 26–23A, 26–25B, 26–26, 26–67A)	43	
42′.	Elytra longer, leaving no more than 1 or 2 abdominal tergites exposed	64	
43(42).	Hind tarsus with 1 less tarsomere than mid tarsus	44	
43′.	Mid and hind tarsi with same number of tarsomeres	47	
44(43).	Body greatly flattened dorsoventrally; abdomen with 5 ventrites (Inopeplinae)	Salpingidae	p. 440
44′.	Body not greatly flattened; abdomen with 6–7 ventrites	45	
45(44′).	Antenna strongly serrate, pectinate, flabellate, bipectinate, or biflabellate	Ripiphoridae	p. 435
45′.	Antenna, at most, very weakly serrate	46	
46(45′).	Pretarsal claw with long, acute process or blade arising from base, usually more than half as long as claw, rarely (*Hornia*) reduced to hyaline spine; antenna filiform; body corpulent and soft	Meloidae	p. 438
46′.	Pretarsal claw simple; antenna weakly clubbed; body cylindrical (Euaesthetinae)	Staphylinidae	p. 409
47(43′).	Eyes large, separated frontally by less than diameter of third antennomere; wings well developed, folded longitudinally at rest; maxillary palp complex; antennomeres 9–11 less than half the width of antennomeres 3–5 (*Atractocerus*)	Lymexylidae	p. 428
47′.	Eyes separated by more than diameter of third antennomere; wings, if well developed, usually folded transversely; maxillary palpi simple; antenna not as in preceding entry.	48	
48(47′).	Scutellary striole present; basal two ventrites connate, suture not diminished medially; antenna of males pectinate to flabellate or plumose; serrate in females	Buprestidae	p. 417
48′.	Scutellary striole absent; ventrites all free or 4 ventrites connate; antenna variable	49	
49(48′).	Antenna with distinct club (Figures 26–5C–I, 26–6A)	50	
49′.	Antenna not clubbed (Figures 26–5A–B)	55[3]	
50(49).	Mid tarsus with 2–4 tarsomeres	Staphylinidae	p. 409
50′.	Mid tarsus with 5 tarsomeres	51	
51(50′).	Antenna with 4 apical antennomeres expanded into asymmetrical club, first shining, other 3 tomentose (Figure 26–6A); elytra usually with some combination of black and orange, but occasionally entirely black (Figure 26–25B); fifth tergite with pair of longitudinal carinae topped by stridulatory files; ≥12 mm long, usually more than 15 mm (Nicrophorinae)	Silphidae[4]	p. 408

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[3] If a mistake is made early in the key, the myxophagan family Hydroscaphidae will key out here. These tiny (length 1.0 to 1.2 mm) beetles can be recognized by the elongate, narrow last antennomere, which does not fit either the "distinct club" or "not clubbed" choice, as well as by the presence of notopleural sutures.

[4] *Thanatophilus* (Silphidae) may key here for individuals with an extended abdomen; it lacks the stridulatory files of the fifth tergite and is 8–14 mm long, but otherwise fits here because of the configuration of the antennae.

51′.	Antenna not as in preceding entry; fifth tergite without stridulatory files; color variable; length 13 mm or less, usually < 10 mm	52	
52(51′).	Antenna with 3 antennomeres; pronotum with antennal pockets anterolaterally above lateral margins; dorsoventrally flattened, louselike parasites of beavers (*Platypsyllus*)	Leiodidae	p. 408
52′.	Antenna with 9–11 antennomeres; pronotum without antennal pockets	53	
53(52′).	Fore coxal cavity open	Staphylinidae	p. 409
53′.	Fore coxal cavity closed	54	
54(53′).	Lateral margins of pronotum complete, that is, with raised flange running from anterior to posterior edge of pronotum; abdomen with 5 ventrites	Nitidulidae	p. 430
54′.	Lateral margins of prontum incomplete; abdomen with 6 ventrites (*Cylidrella*)	Trogossitidae	p. 428
55(49′).	Mid tarsus with 4 or fewer tarsomeres	Staphylinidae	p. 409
55′.	Mid tarsus with 5 tarsomeres	56	
56(55′).	Mesosternum medially excavated, forming a cavity to receive extended prosternal process; U.S. Southwest (Cebrioninae)	Elateridae	p. 422
56′.	Mesosternum not excavated to receive extended prosternal process; widespread in distribution	57	
57(56′).	Antenna with 12 antennomeres; antenna biserrate, bipectinate, or biramose (Figure 26-46B)	Phengodidae	p. 423
57′.	Antenna with fewer than 12 antennomeres; antennal type variable	58	
58(57′).	Last maxillary and labial palpomeres long, nearly as long as, or longer than, antenna	Telegeusidae	p. 423
58′.	Last maxillary and labial palpomeres much shorter than antenna	59	
59(58′).	Head covered above by pronotum (Figure 26–47A); often with luminous organs on abdomen	Lampyridae	p. 423
59′.	Head visible from above; never with luminous organs	60	
60(59′).	Anterior edge of scutellum abruptly elevated, with distinct step to mesoscutum (female *Anorus*)	Dascillidae	p. 417
60′.	Anterior edge of scutellum in same plane as mesoscutum.	61	
61(60′).	Pronotum with lateral eversible vesicles (Malachiinae)	Melyridae	p. 429
61′.	Pronotum without eversible vesicles	62	
62(61′).	Hind wing rolled cigarlike; median setose cavities present on male ventrites 3–5; trochantin concealed; scutellum emarginate posteriorly; <3 mm long	Micromalthidae	p. 401
62′.	Hind wing, if fully developed, folded normally; ventrites without setose cavites; trochantin exposed or concealed; scutellum variable; length variable	63	
63(62′).	Elytra individually rounded, not meeting apically at suture; mandible long and narrow	Cantharidae	p. 424
63′.	Elytra truncate, meeting at suture apically; mandible often short and broad	Staphylinidae	p. 409
64(42′).	Apices of penultimate 2 or 3 antennomeres each completely ringed with microsetose groove (periarticular gutters) (must be viewed distally, difficult to see in very small specimens or in those with very compact antennal club); antenna with distinct to indistinct loose club; prothorax with sharp lateral margins; abdomen with 5–6 ventrites; fore trochantin exposed or hidden, if hidden and antenna with 11 antennomeres, then antennomere 8 smaller than 7 or 9 (Figure 26–4)	65	

64′.	Antenna usually lacking periarticular gutters on antennal club; other characters variable; if complete periarticular gutters present, then fore trochantin hidden, antenna with 11 antennomeres, and antennomere 8 not smaller than 7 and 9	66	
65(64).	Hind tibial spurs subequal in length; small (1–6 mm), round to elongate-oval, shining, granulate or transversely strigulate beetles; elytra glabrous or pubescent, striate or not; prothorax as broad as elytra; fore coxa strongly projecting and constricted by coxal cavity; often capable of retracting into a ball shape by curling head and prothorax under body; antenna distinctly clubbed, often with 11 antennomeres, 5 of which are involved in club and antennomere 8 smaller than 7 or 9. Some genera with 10 or 11 antennomeres and with distinct club of 3 or 4 antennomeres; these with flattened, externally flanged hind femur, apical portion excavate to receive tibia; tarsal formula highly variable, 3-3-3, 4-4-4, 5-4-4, 5-5-4 or 5-5-5; one genus (*Colon*) with 11 antennomeres and somewhat gradually clubbed antenna that lacks small eighth antennomere, elytra pubescent, with characteristic shape and sutural stria (see also couplet 124)	Leiodidae[5]	p. 408
65′.	Hind tibial spurs distinctly unequal; moderately sized (4–14 mm), somewhat flattened shining beetles; elytra striate and glabrous; pronotum somewhat narrowed relative to elytra; fore coxa strongly projecting or transverse; body not retractile; antenna long, club loose and indistinct, eighth antennomere never smaller than 7 and 9; femur simple; tarsi 5-5-5	Agyrtidae	p. 408
66(64′).	Mid tarsus with 3 apparent tarsomeres, either clearly with 3 tarsomeres (Figure 26–10I), or second tarsomere strongly lobed and hiding small penultimate (third) tarsomere (Figure 26–10E)	67	
66′.	Mid tarsus with 4 or 5 distinct tarsomeres, or first tarsomere distinctly lobed, engulfing very small second and small third of 4 tarsomeres, thus appearing to have 2 or 3 tarsomeres	75	
67(66).	Mid tarsus pseudotrimerous, with second tarsomere strongly lobed, hiding small penultimate (third) tarsomere (Figure 26–10E)	68	
67′.	Mid tarsus truly with three tarsomeres, second tarsomere not greatly lobed	70	
68(67).	Fore coxal cavity closed (except in *Holopsis*); head small, usually covered by hoodlike pronotum; if head exposed from above, fore coxal cavities closed; mostly tiny beetles <2 mm	Corylophidae	p. 434
68′.	Fore coxal cavity open; head visible from above in front of pronotum; size variable, up to 11 mm	69	
69(68′).	Frontoclypeal suture distinctly impressed; all ventrites free; first ventrite without postcoxal lines; pronotum often with sublateral lines (Figure 26–59C)	Endomychidae	p. 433
69′.	Frontoclypeal suture absent; 2 basal ventrites connate, first ventrite with postcoxal lines; pronotum lacking sublateral lines	Coccinellidae	p. 433
70(67′).	Eyes absent (*Anommatus*)	Bothrideridae	p. 433
70′.	Eyes present	71	
71(70′).	Head gradually narrowed behind eyes, without distinct temples or neck; fore coxal cavity open; body oval or elongate oval with base of pronotum subequal in width to elytral base	72	

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[5] Three very aberrant and ecologically restricted genera that lack distinctly clubbed antennae belong here. *Glacicavicola* is restricted to ice caves in Idaho and Wyoming and characterized by elongate head, pronotum and elytra, each separately constricted; cuticle translucent, shining; eyes absent, and with elongate, slender legs and antennae. Two genera of Platypsyllinae are associated with mammals and their nests and are characterized by oval body, strongly flattened dorsoventrally, recumbent pubescence, an occipital crest overlapping anterior margin of pronotum and eyes absent or barely indicated.

71′.	Head sharply narrowed behind eyes or temples, with distinct neck; fore coxal cavity open or closed; body elongate or elongate oval, with base of pronotum distinctly narrower than elytra	73	
72(71).	Antennal scape normal, shorter than club; funicle longer than entire club; posterior edge of last ventrite crenulate (*Ostomopsis*)	**Cerylonidae**[6]	p. 433
72′.	Antennal scape large, subequal to length of club; funicle with 3 antennomeres, shorter than first antennomere of club (*Micropsephodes*)	**Endomychidae**	p. 433
73(71′).	Abdomen with 6 ventrites; head narrowed immediately behind eyes, lacking temples; fore coxal cavity open; lateral margin of pronotum coarsely dentate; trochantin exposed; mid coxal cavity open (*Dasycerus*)	**Staphylinidae**	p. 409
73′.	Abdomen with 5 ventrites; head behind eyes with distinct temples; fore coxal cavity open or closed; lateral margin of pronotum simple to finely dentate or absent; trochantin concealed; mid coxal cavity variable	74	
74(73′).	Abdomen very short, one half length of metasternum; pronotum not margined laterally; scutellum not visible; elytron at base with pit at end of impressed groove; Florida	**Jacobsoniidae**	p. 424
74′.	Abdomen longer than metasternum; (except *Akalyptoischion*, California); lateral margin of pronotum absent to finely dentate; scutellum small but visible; elytra usually striate; common and widespread	**Latridiidae**	p. 434
75(66′).	Antenna with 9 antennomeres, last 5 involved in club; abdomen with 6–7 ventrites; tiny intercoxal sclerite present between hind coxae; maxillary palp long relative to antenna; ventral surface with water-repellent pubescence; ≤3.0 mm length	**Hydraenidae**	p. 408
75′.	Without the preceding combination of characters	76	
76(75′).	Antenna with 7–9 antennomeres, antennomeres 7–9 usually forming loose, tomentose club, antennomere 6 often forming a cupule at base of club; maxillary palp often as long or longer than antenna (Figure 26–22), always longer than half antennal length; hind coxa with ventroposterior carina setting off convex posterior face that rotates against anterior excavation of first ventrite; planes of ventral surface of hind coxa and first ventrite discontinous; hind trochanter inserted on ventral (not posterior) surface of coxa (Figure 26–22B), femur held against ventral face of coxa, not against posterior face of coxa, or flat to abdominal surface when fully retracted	**Hydrophilidae**	p. 406
76′.	Antenna variable but not as in preceding entry; maxillary palp usually much shorter than antenna; hind coxa configured differently	77	
77 (26′,76′).	Hind coxa with distinct posterior face (at least medially) set off from ventral surface by carina or flange, posterior face often excavated; ventral surface of hind coxa not continuous with first ventrite; hind femur inserted on posterior face of coxa, held posterior to coxa when retracted; fore coxal cavity open; mid and hind tarsi with equal number of tarsomeres	78	
77′.	Hind coxa without distinct posterior face; hind trochanter often inserted on ventral surface or on small medial projection of coxa, never received in coxal excavation and resting ventrad of coxa in retracted position; ventral surface of hind coxa more or less continuous with first ventrite, or, if not, then hind tarsus with 1 fewer tarsomere than mid tarsus; fore coxal cavity open or closed	118	

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[6] The myxophagan family Microsporidae will key out here if a mistake is made in couplet 2. They match the antennal characters in this couplet but lack the crenulation on the last ventrite. These tiny (length 0.5–1.2 mm) beetles can be easily recognized by having only three ventrites (five in *Ostomopsis*).

78(77).	Abdomen with 7–8 ventrites, hind tarsus with 5 tarsomeres	79	
78′.	Abdomen with 6 or fewer ventrites; hind tarsus with 5 or 4 tarsomeres	84	
79(78).	Head with median ocellus (*Thylodrias*)	Dermestidae	p. 424
79′.	Head without median ocellus	80	
80(79′).	Antenna with 12 antennomeres, biramose (male *Zarhipis*)	Phengodidae	p. 423
80′.	Antenna with 11 antennomeres, simple to uniramose or biramose	81	
81(80′).	Mid coxae distinctly separated; elytra often reticulate (Figure 26–46A), at least feebly costate; femur or tibia compressed; pronotum with distinct longitudinal median carina, groove, or cell, occasionally restricted to base or disc	Lycidae	p. 422
81′.	Mid coxae contiguous or nearly so; elytra not reticulate; femur and tibia seldom compressed; pronotum rarely with distinct longitudinal median carina, groove, or cell	82	
82(81′).	Pronotum extended forward, covering head in dorsal view; 1 or more ventrites often with luminous organs (most obvious in males); antennal insertions separated by distance ≤ diameter of antennal fossa	Lampyridae	p. 423
82′.	Head exposed in dorsal view when extended; if covered by pronotum, then antennae separated by nearly 2× diameter of antennal fossa; abdomen lacking luminous organs	83	
83(82′).	Labrum not distinct, membranous and often hidden beneath clypeus; abdomen with paired glandular openings on lateral edge of tergites; tarsomere 4 with bifid ventral lobe	Cantharidae	p. 424
83′.	Labrum distinct and sclerotized; abdomen lacking paired glandular openings on tergites; tarsomeres 3 and 4 with bifid ventral lobes	Omethidae	p. 424
84(78′).	Posterior angles of prothorax acute, embracing elytral humeri (Figure 26–45A,C,D); hind tarsus with 5 tarsomeres; 3 or more ventrites connate; prothorax dorsoventrally mobile relative to mesothorax; intercoxal process of prosternum long, notched dorsally; received in deep mid-coxal cavity as a clicking mechanism; if clicking mechanism cannot be seen because visible portion of intercoxal process is flat ventrally and received tightly in deeply emarginate mesosternum, then sternopleural suture or hypomeron grooved to receive antenna	85	
84′.	Posterior angles of prothorax not acute and embracing elytral humeri, or rarely somewhat acute and weakly embracing humeri; hind tarsus with 5 or 4 tarsomeres; ventrites variable; prosternal process variable, but if large and received in deeply emarginate mesosternum, apex of prosternal process not notched dorsally nor capable of clicking; if large prosternal process received tightly in deep mid-coxal cavity and underside of prothorax grooved to receive antenna, then hind tarsus with 4 tarsomeres	87	
85(84).	Labrum not externally visible; abdomen with 5 connate ventrites	Eucnemidae	p. 421
85′.	Labrum free and visible; abdomen with 3–5 connate ventrites	86	
86(85′).	Antenna indistinctly to distinctly clubbed, apex received in margined cavity on posterolateral portion of hypomeron, just anterior to retracted fore leg; metasternum with or without oblique margined groove for mid tarsus; prosternum with click mechanism hidden by platelike ventral surface of postcoxal intercoxal process, which fits tightly against exposed portion of mesosternal cavity; elytra strongly striate and covered with silky, subrecumbent setae; abdomen with 5 connate ventrites; length 1–5 mm	Throscidae	p. 422

86′.	Antenna variable (filiform, serrate, pectinate, etc.), but not clubbed; antennal groove, if present, at or near sternopleural suture; metasternum without margined groove for mid tarsus; if click mechanism hidden as in preceding entry, elytra not strongly striate and setae suberect; abdomen with 3 or 4 connate ventrites; length 1–60 mm (Figure 26–45A,C,D)	Elateridae	p. 422
87(84′).	Either mid coxal cavity closed laterally, the mesosternum and metasternum meeting laterad of mid coxa; or antenna elongate, antennomeres 3–8 with long rami, 9–11 flattened, elongate-serrate; pronotum often hoodlike, covering head from above (Figures 26–50, 26–53)	88	
87′.	Mid coxal cavity open laterally, mesosternum and metasternum separated laterad of mid coxa by the mesepimeron, or mesepimeron and mesepisternum; antenna not as in preceding entry; pronotum variable	89	
88(87).	Hind trochanter cylindrical, short to long, squarely attached to femur, distinctly separating coxa and tibia	Anobiidae	p. 427
88′.	Hind trochanter short, triangular, obliquely attached to femur so that femur and coxa are adjacent or narrowly separated on one side	Bostrichidae	p. 426
89(87′).	Either anterior margin of scutellum with abrupt, carinate elevation that fits against posterior margin of pronotum, or scutellum absent or not visible	90	
89′.	Scutellum visible, anterior margin not abruptly elevated, fitting under overlapping posterior margin of pronotum	113	
90(89).	Fore coxa strongly and distinctly projecting below prosternum, one third or more of dorsoventral length below intercoxal process; fore coxa usually conical or transversely conical	91	
90′.	Fore coxa not or weakly projecting below prosternum; if fore coxa conical, then lying longitudinally and not or weakly projecting ventrally below intercoxal process	98	
91(90).	Tarsi with 4 distinct tarsomeres; hind coxal plates greatly expanded, hiding most of first ventrite; hind wing, when developed, often fringed with long setae; length 0.7–2 mm	Clambidae	p. 417
91′.	Tarsi with 5 distinct tarsomeres; hind coxal plates distinct but not hiding most of first ventrite; wing not fringed; size variable	92	
92(91′).	Antenna with distinct, simple club of 3 antennomeres (Figure 26–5G)	93	
92′.	Antenna variously constructed, but without a simple club of 3 compact antennomeres	95	
93(92).	Elytra truncate; pygidium sclerotized and completely or nearly completely exposed	Sphaeritidae	p. 407
93′.	Elytra complete; pygidium not sclerotized, completely covered or with only small portion exposed	94	
94(93′).	Upper surface of body glabrous; body contractile; fore tibia held anterior to femur, covering antenna in hypomeral cavity when contracted (Orphilinae)	Nosodendridae	p. 424
94′.	Upper surface of body variously pubescent, setose or scaled; body not strongly contractile; fore tibia held posterior to femur, antennal club not covered by leg when contracted	Dermestidae	p. 424
95(92′).	Base of pronotum crenulate; scutellum usually medially notched on anterior margin; antennal insertion not elevated; mandible moderate and evenly curved; labrum large, sclerotized, and dorsal to mandibles	Ptilodactylidae	p. 420

95′.	Base of pronotum simple; anterior margin of scutellum not notched; dorsal margin of antennal insertion elevated and protuberant; mandible large, abruptly curved mesad at nearly right angle; labrum either short and membranous or extending between and below mandibles	96	
96(95′).	Empodium hidden between bases of claws or absent; base of pronotum nearly straight (Figure 26–35C)	Dascillidae	p. 417
96′.	Empodium large, one third length of claw; base of pronotum strongly sinuate around scutellum (Figure 26–36)	97	
97(96′).	Tarsomeres 1–4 with large, membranous, divided lobes (Figure 26–10F); antenna lamellate (males) or increasingly serrate apically (females)	Rhipiceridae	p. 417
97′.	Tarsi simple, without ventral lobes; antenna serrate to pectinate	Callirhipidae	p. 421
98(90′).	Head with single median ocellus	Dermestidae	p. 424
98′.	Head without ocellus	99	
99(98′).	Antenna short, not reaching middle of pronotum, scape and pedicel (antennomeres 1–2) relatively large, together one third or more of total length; antennomeres 3 to last transverse; body covered in dense tomentum	100	
99′.	Antenna short to long, scape and pedicel (antennomeres 1–2) not one third of total length; antennomeres 3 to last variable; body vestiture variable	102	
100(99).	Head distinctly prognathous, mandibles strongly projecting forward (Figure 26–43A); fore femur widened medially and armed externally with strong spines (Figure 26–43A); mid tarsus with 4 tarsomeres	Heteroceridae	p. 420
100′.	Head distinctly hypognathous, mandibles either directed ventrad or hidden (Figure 26–43B); fore femur simple, neither widened medially nor armed with large spines; mid tarsus with 5 tarsomeres	101	
101(100′).	Metasternite with postcoxal lines delimiting retractile position of mid tibia; antenna hidden in subocular groove and cavity between head and pronotum; body oval	Lutrochidae	p. 420
101′.	Metasternite without postcoxal lines; subocular groove absent or very weakly developed, antenna not hidden in pronotum; body nearly parallel-sided (Figure 26–43B)	Dryopidae	p. 420
102(99′).	Scape and pedicel received in deeply excavate pro- and mesosterna between fore and mid coxae; pedicel longer than scape, scape and pedicel together more than two thirds length of serrate flagellum; body strongly contractile, all legs received in cavities; mid tarsus with 5 tarsomeres, with long lobe on third tarsomere, fourth small and sometimes difficult to see (pseudotetramerous)	Chelonariidae	p. 421
102′.	Antenna not received in excavation between fore and mid coxa; antenna not as in preceding entry; mid tarsus usually not pseudotetramerous	103	
103(102′).	Head with subgenal ridges that fit against fore coxae when head deflexed	Scirtidae	p. 417
103′.	Head without subgenal ridges, genae not in contact with fore coxae	104	
104(103′).	Two basal ventrites connate, either with suture between them partially obliterated medially or, if suture between ventrites 1 and 2 not medially indistinct, sternopleural sutures at least moderately grooved to receive antennae	105	

104′.	Ventrites all free, or 3 or 5 ventrites connate; ventrite sutures and sternopleural sutures variable	106	
105(104).	Suture between 2 basal ventrites distinct medially; mid tarsus with small, bisetose empodium; antenna filiform to distinctly clubbed; body strongly convex	Byrrhidae	p. 417
105′.	Suture between 2 basal ventrites weak to absent medially (Figure 26–8B); mid tarsus lacking visible empodium; antenna usually serrate, pectinate, or flabellate; body weakly flattened dorsoventrally	Buprestidae	p. 417
106(104′).	Legs retractile, rotated forward in repose, with tibia held anterior to femur; fore femur with flange on posterior face covering tibial excavation, fore tibia grooved to receive tarsus; usually with margined excavations on propleuron, mesosternite and ventrites to receive legs	107	
106′.	If legs retractile, fore tibia held posterior to or ventral to femur; fore femoral flange, if present, located on anterior face	108	
107(106).	Mentum strongly sclerotized, expanded, covering labium and maxillae; head not deflexible; antenna covered by fore legs in broad sternopleural pocket; ventrites 1 and 2 excavate for hind leg; mid tibia with marginal spines; length 4–9 mm	Nosodendridae	p. 424
107′.	Mentum normal, head usually retractable into pronotum to anterior margin of eyes (1 exception); antenna received in internal pronotal cavity beneath head, external anterior pronotal cavity or partly in sternopleural grooves and partly under legs against hypomeron; excavation for hind leg, if present, limited to ventrite 1; margin of mid tibia not spinose; length 1–2 mm	Limnichidae	p. 420
108(106′).	Elytra with thumblike process on inner lateral surface near subapical curve, locking into ventrite (elytra must be separated from side of abdomen to see this character)	Artematopodidae	p. 421
108′.	Elytra without such a locking device	109	
109(108′).	Posterior angles of pronotum with short discal carinae; fore coxal cavity with narrow lateral extension at pleurosternal suture	Brachypsectridae	p. 421
109′.	Posterior angles of pronotum without short discal carinae; fore coxal cavity broad at pleurosternal suture	110	
110(109′).	Propleuron extended mesad behind fore coxa for approximately half length of trochantin; length 10–15 mm	111	
110′.	Margin of propleuron curved laterad posteriorly, not extended mesad posterior to fore coxa; length 1–8 mm	112	
111(110).	Posterior margin of pronotum crenulate; mid tibial spines subequal in size, smooth; antenna compressed serrate; tarsomeres simple; empodium large and setose	Eulichadidae	p. 421
111′.	Posterior margin of pronotum simple; mid tibial spines unequal in size, finely serrate; antenna cylindrical-serrate (Figure 26–35C); tarsomeres 1–4 with large, divided membranous lobes; empodium absent	Dascillidae	p. 417
112(110′).	Posterior edge of pronotum simple; last tarsomere much longer than others, usually half or more total length of tarsus	Elmidae	p. 419
112′.	Posterior edge of pronotum crenulate; last tarsomere subequal in length to first	Psephenidae	p. 420
113(89′).	Head with subgenal ridges that fit against fore coxae when head deflexed; prosternum in front of coxa narrow, shorter than intercoxal process	Scirtidae	p. 417

113′.	Head without subgenal ridges, genae usually not in contact with fore coxae; prosternum in front of coxa nearly as long as or longer than intercoxal process	114	
114(113′).	Hind coxal plate large, platelike, longer medially than metasternite, hiding most of hind femur, even when fully extended	Eucinetidae	p. 416
114′.	Hind coxal plate narrow, forming either a parallel plate or simple carina; hind femur fully visible	115	
115(114′).	Length of body ≥4× maximum width; male maxillary palp complex, multilobate	Lymexylidae	p. 428
115′.	Length of body ≤2.5× maximum width; maxillary palp not branched	116	
116(115′).	Prosternal intercoxal process complete, reaching behind fore coxa to level of mesosternum; posterior portion of hypomeron not extending behind fore coxa; elytral epipleuron with an internally carinate edge complete to suture; head with face narrowed; clypeal margin straight; 3 basal ventrites connate	Psephenidae	p. 420
116′.	Prosternal intercoxal process incomplete, not reaching beyond midpoint of fore coxa; posterior portion of hypomeron variable behind fore coxa; elytral epipleuron narrowed before reaching suture (complete in 1 genus); head with face not greatly narrowed; clypeal margin emarginate; all ventrites free	117	
117(116′).	Elytra with 9 or 10 punctate striae; posterior portion of hypomeron extending up to half the distance to mesal edge of fore coxa; length 7–14 mm	Agyrtidae	p. 408
117′.	Elytra without punctate striae, otherwise variable, irregularly punctate (Figure 26–25B), with complex low sculpture (Figure 26–25A) or up to 3 carinate costae; posterior portion of hypomeron not extending behind fore coxa or extending only a short distance mesad of lateral edge of fore coxa; length 7–45 mm	Silphidae	p. 408
118(77′).	Hind coxae widely separated by broad, truncate intercoxal process of first ventrite	119	
118′.	Intercoxal process of first ventrite absent, acute or rounded	121	
119(118).	Mid coxal cavity open laterally, closure involving mesepisterna (Georissinae)	Hydrophilidae	p. 406
119′.	Mid coxal cavity open or not, if open, then closure solely involving mesepimeron	120	
120(119′).	Antenna geniculate, club usually of 3 antennomeres; elytra short and truncate, exposing two nonflexing terga; body compact (Figure 26–23A)	Histeridae	p. 407
120′.	Antenna not obviously geniculate, with or without club; elytra rarely exposing 2 terga, if 2 terga exposed, then exposed abdominal segments flexible; body not oval or body cylindrical and compact	121	
121 (118′,120′).	Fore coxa with exposed trochantin	122	
121′.	Trochantin concealed or absent	140	
122(121).	Hind coxa extending laterally to reach elytral epipleuron or side of body, no visible contact between metathorax and first ventrite	123	
122′.	Hind coxa not reaching elytron; first ventrite and metathorax visibly in contact laterad of coxa (Figures 26–8A,B)	128	
123(122).	Hind tarsus with 5 tarsomeres	124	

123′.	Hind tarsus with 4 tarsomeres	169	
124(123).	Head with temples and occipital ridge distinct, occipital ridge closely fitting against pronotum, constricted behind to a distinct neck (difficult to see when head is retracted with ridge and temples against pronotum); elytra with strong characteristic sutural stria, no other striae evident; 11 antennomeres, gradual club of 3–4 antennomeres; abdomen with 4 (females) or 5 (males) ventrites (*Colon*, see couplet 65)	Leiodidae	p. 408
124′.	Head without ridge and constricted neck that fits against pronotum; elytra striate or not, but not as in preceding entry; antenna variable; at least 5 ventrites	125	
125(124′).	Prosternal process between coxae distinctly elevated above level of prosternum, apex strongly curved dorsally, reaching level of postcoxal extensions of hypomeron; cervical sclerites absent; antenna not clubbed; elytra glabrous or subglabrous; length 8–20 mm	Cerambycidae	p. 441
125′.	Prosternal process not elevated between coxae nor with apex strongly curved dorsad; cervical sclerites present; antenna clubbed or not; elytra densely to sparsely setose, subglabrous or glabrous; length 1–24 mm	126	
126(125′).	Fore coxa not projecting distinctly below intercoxal process, large and transverse; antenna distinctly clubbed; prothorax with sharp lateral margins; if fore coxa slightly projecting, then antenna distinctly clubbed, tarsi not lobed beneath, not bright red	Trogossitidae	p. 428
126′.	Fore coxa projecting distinctly below intercoxal process, conical or transverse; antenna variable; margins of prothorax variable; if fore coxa are only slightly projecting, then antenna feebly clubbed, tarsi lobed beneath, body bright red	127	
127(126′).	Tarsi not lobed beneath; fore coxal cavity strongly transverse; labrum subtruncate to convex, rounded or acute; eye not emarginate; antenna rarely with distinct apical club, and if so, club of 5 or more antennomeres; elytra usually confusedly punctate; pronotum and abdomen sometimes with eversible glands	Melyridae	p. 429
127′.	Tarsi with lobes on multiple tarsomeres; fore coxal cavity circular, elongate or slightly transverse; labrum subtruncate to concave or deeply emarginate; eye often emarginate; antenna usually apically clubbed, club of one or more antennomeres; elytra often punctate-striate; pronotum and abdomen never with eversible glands	Cleridae	p. 428
128(122′).	Elytra short, completely exposing 1 or more tergites	129	
128′.	Elytra covering all of abdomen or exposing apex of 1 tergite	132	
129(128).	Fore coxal cavity broadly open (by more than half width of coxa); labium with 2 palpomeres; abdominal process truncate; pygidium and last ventrite longer than preceding 4 combined	Smicripidae	p. 430
129′.	Fore coxal cavity closed or narrowly open by less than half width of coxa; labium with 3 palpomeres or nonarticulated; abdominal process acute to broadly rounded or absent; pygidium variable	130	
130(129′).	Labial palps nonarticulated; prosternal process elevated between fore coxae and strongly curved dorsally behind	Brachypteridae	p. 429
130′.	Labium with 3 palpomeres; prosternal process flat or elevated between fore coxae, but not strongly curved dorsally behind	131	
131(130′).	Antenna with 10 antennomeres, club of only one antennomere; elytra >2× as long as wide (Rhizophaginae)	Monotomidae	p. 430

131′.	Antenna with 10 or 11 antennomeres, club of 3 or more antennomeres; elytra <2× as long as wide	Nitidulidae	p. 430
132(128′).	Mid tarsus with 4 tarsomeres; tarsal lobes, if present, small, not obscuring penultimate tarsomere	133	
132′.	Mid tarsus with 5 tarsomeres, fifth possibly obscured by enlarged lobe of fourth (pseudotetramerous)	135	
133(132).	Lateral margin of pronotum crenulate; antennal insertions concealed from above (*Sphindocis*)	Ciidae	p. 434
133′.	Lateral margins of pronotum smooth or minutely denticulate; antennal insertions visible from above	134	
134(133′).	Body nearly spherical, capable of being rolled into a ball; mandibles resting against metasternum in retracted position (*Cybocephalus*)	Nitidulidae	p. 430
134′.	Body flattened cylindrical, not at all spherical (Figure 26–60A) (Mycetophaginae)	Mycetophagidae	p. 434
135(132′).	Antenna with 10 antennomeres, 1 involved in club (Rhizophaginae)	Monotomidae	p. 430
135′.	Antenna with 10 or 11 antennomeres, if clubbed, club of 2 or more antennomeres	136	
136(135′).	Body extremely flattened; elytra nearly parallel-sided, disc almost perfectly flat between rounded lateral carinae running from humeri to near apex, setting off vertical sides and guttered epipleural margin; either large (>10 mm) and red with expanded temples (Figure 26–58A), or small (<5 mm) and dull brown without temples	Cucujidae	p. 431
136′.	Body not so distinctly flattened; elytra distinctly transversely arched; not fitting other combinations in preceding entry	137	
137(136′).	Dorsal face of mandible with tubercle that fits into cavity on clypeus, setose cavity at base, hidden when mandibles are closed (mycangium); elytra with scutellary striole; antenna with 2 or 3 antennomeres forming club; body oval to cylindrical	Sphindidae	p. 429
137′.	Mandible without dorsal mycangium; elytra without scutellary striole; antenna and body shape variable	138	
138(137′).	Mid and hind tarsi with equal numbers of tarsomeres; antenna with distinct club	139	
138′.	Hind tarsus with 1 tarsomere less than mid tarsus; antenna distinctly clubbed or not	169	
139(138).	Pygidium at least partially exposed, strongly sclerotized, punctate, distinctly different from other tergites (Figures 26–57A,B); tibiae usually spinose or denticulate on external margin	Nitidulidae	p. 430
139′.	Pygidium not exposed, not strongly sclerotized, similar to other tergites (Figure 26–60B); tibiae smooth on external margin	Byturidae	p. 432
140(121′).	Antennal insertions concealed from above by lateral expansion of frons; three basal ventrites connate, fourth and fifth movable; fore coxal cavity closed by mesad extension of posterior portion of the hypomeron; fore coxal process not expanded laterally at apex to close fore coxal cavity; antenna usually with 11 antennomeres (rarely with 9 or 10 antennomeres)	Tenebrionidae	p. 436
140′.	Without this combination of characters	141	
141(140′).	Abdomen with first 4 ventrites connate	142	
141′.	Abdomen with fewer than 4 ventrites connate	143	

142(141).	Antenna serrate or pectinate; antennal insertion exposed from above; hind coxa laterally reaching epipleuron; intercoxal process of prosternum with long, notched, apical projection, received in deep mesosternal cavity to form clicking mechanism; last ventrite without submarginal groove; mentum without setose pit	Cerophytidae	p. 421
142′.	Antenna moniliform, clavate, or capitate; antennal insertion concealed from above; hind coxa not reaching elytron, first ventrite and metepimeron in contact laterad of coxa and mesad of epipleuron; prosternal process broad, widened apically; last ventrite usually with submarginal groove; males often with median setose pit on mentum	Zopheridae	p. 435
143(141′).	Hind tarsus with 5 tarsomeres, basal tarsomere reduced, often difficult to see, either hidden in apical excavation of hind tibia or shorter than fourth length of second tarsomere and obliquely attached beneath it (may only be visible from below in oblique distal angle, see Figure 26–10D); elytra covering pygidium	Bostrichidae	p. 426
143′.	First tarsomere usually not so reduced; if so, then pronotum not hoodlike, head not hypognathous or hind tarsus of 4 tarsomeres, pygidium exposed	144	
144(143′).	Mid tarsus with 4 distinct tarsomeres	145	
144′.	Mid tarsus with 5 tarsomeres, or tarsus pseudotetramerous	156	
145(144).	Mid coxal cavity closed laterally	146	
145′.	Mid coxal cavity open laterally	152	
146(145).	Antennal insertion concealed from above	147	
146′.	Antennal insertion exposed from above	148	
147(146).	Eyes usually present; if eyes absent, then elytra with flat tubercles	Colydiidae	p. 435
147′.	Eyes absent, elytra smooth (*Aglenus*)	Salpingidae	p. 440
148(146′).	Genae with pair of anteriorly directed horns extending beyond labium, horns visible from above	Prostomidae	p. 437
148′.	Genae lacking horns	149	
149(148′).	Abdomen with 6 ventrites; pronotum usually large, hoodlike, covering or nearly covering head; pygidium usually exposed; epipleuron incomplete; frontoclypeal suture absent; length <2 mm	Corylophidae	p. 434
149′.	Abdomen with 5 or 6 ventrites, if 6, then length ≥4 mm and frontoclypeal suture present; pronotum never hoodlike, head visible from above; pygidium and epipleuron variable	150	
150(149′).	Antenna long, reaching to or beyond middle of pronotum, club loose; pronotum usually with pair of sublateral discal carinae or grooves, running from base laterad of basal pits (Figure 26–59C); body usually round to ovoid	Endomychidae	p. 433
150′.	Antenna short, not reaching beyond middle of pronotum, club compact; if pronotum with discal carinae or grooves, then usually in the form of a median groove or pit and body elongate	151	
151(150′).	Either posterior margin of last ventrite crenulate or body distinctly oval, length no more than 2× maximum width; antenna with 8–10 antennomeres; hind trochanter obliquely attached to femur, but distinctly separating coxa from femur	Cerylonidae	p. 433
151′.	Posterior margin of last ventrite never crenulate; body elongate, at least 2.75× maximum width; antenna with 10–11 antennomeres; hind trochanter offset so that femur and coxa are in contact or nearly so	Bothrideridae	p. 433

152(145′).	Hind coxae separated by distance $>\frac{1}{2}$ transverse diameter	153	
152′.	Hind coxae separated by distance $<\frac{1}{2}$ transverse diameter	154	
153(152).	Fore coxal cavity narrowly closed; fore and mid coxae strongly transverse; mandible tucked into cavity when closed, not visible from side; antenna with 9 antennomeres, last 5 forming club; pronotum not grooved or carinate on disc; small beetles, <2 mm long (*Orthoperus*)	Corylophidae	p. 434
153′.	Fore coxal cavity narrowly to widely open; fore and mid coxae circular to slightly transverse; mandible visible from side; antenna with 8–11 antennomeres, if clubbed, club of 1–3 antennomeres; pronotum usually with submarginal grooves or carinae, especially basally (Figure 26–59C); size 1–10 mm, if <2 mm and lacking grooves or carinae on pronotum (*Eidoreus*), then antenna with 10–11 antennomeres, 1 or 2 of which form a distinct club	Endomychidae	p. 433
154(152′).	Intercoxal process of first ventrite absent, no part of ventrite extending between coxae to contact metasternite; first ventrite lacking margined hind coxal cavities; hind coxa conical and projecting; body soft; small, triangular part of true abdominal sternite 2 usually visible laterad of hind coxa (that is, ventrite 1 small, divided); often colorful, with red, yellow or metallic blue or green markings; length 5–12 mm (Psoinae)	Bostrichidae	p. 426
154′.	Intercoxal process of first ventrite complete; first ventrite with margined coxal cavities; hind coxa transverse; body fully sclerotized, ventrite 1 closing anterolateral angle between hind coxa and abdomen; never metallic; length 0.5–6.5 mm	155	
155(154′).	Body elongate-oval and somewhat cylindrical; pronotum usually very convex in transverse section, edges often directed ventrally; pronotum without basal pits or impressions; head or pronotum of male often with horns or tubercles; antenna with 8–10 antennomeres and club of 2–3 antennomeres; males often with pubescent median fovea on first ventrite; head without distinct temples or neck	Ciidae[7]	p. 434
155′.	Body oval to elongate-oval, usually somewhat dorsoventally depressed; pronotum usually weakly convex transversely, edges directed laterally; pronotum with 2 basal pits or impressions laterad of scutellum, sometimes in posterior marginal groove and difficult to discern; head and pronotum without horns or tubercles; antenna with 11 antennomeres, last 2–5 forming club; all ventrites free, without median fovea	Mycetophagidae[8]	p. 434
156(144′).	Abdomen with 6 ventrites; hind tarsus with 5 tarsomeres; terminal maxillary palpomere (4) shorter and narrower than penultimate; shape rather characteristic (Figure 26–24B); length 0.6–2.7 mm	Scydmaenidae	p. 408
156′.	Abdomen with 4–5 ventrites; hind tarsus variable; terminal maxillary palpomere (3 or 4) as wide or wider or as long or longer than penultimate; size variable	157	
157(156′).	Pregular area on each side with a lateral-facing surface bearing setose pit or cavity near end of distinct antennal groove; first ventrite with postcoxal lines	Biphyllidae	p. 433
157′.	Pregular area without lateral-facing setose pit; antennal grooves and postcoxal lines variable	158	

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[7] One species from California has relatively flat pronotum with crenulate margins directed laterally, antenna with 11 antennomeres and 3 antennomeres in club, but two basal sternites are connate.

[8] One rare genus (length <2 mm) somewhat cylindrical, with very convex pronotum in transverse section, with head abruptly constricted behind short temples to form distinct neck.

158(157′).	First ventrite much longer than second, measured behind coxa; elytra without punctate or impressed striae (traces of striae occasionally visible through cuticle but not expressed on the surface); epipleuron distinct in basal half, not reaching apex, usually narrowed at level of third ventrite; gena carinate and projecting ventrally between eye and mentum; apex of elytra with double suture or "subapical gap" caused by wide flange of elytral coupling system; elytra complete, exposing at most tip of last tergite	Cryptophagidae[9]	p. 431
158′.	Not fitting this combination of characters, either with the first ventrite short, elytra striate, epipleuron complete to apex, gena flat between eye and mentum, or elytra not covering most of pygidium	159	
159(158′).	Hind trochanter transversely or obliquely attached to femur, but distinctly separating femur from coxa (Figures 26–9A–E)	160	
159′.	Hind trochanter obliquely attached to femur, offset so that femur abuts coxa	169	
160(159).	Antennal insertions approximated or separated by less than half width of head behind eyes; pronotum without lateral carinae; hind tarsus with 5 tarsomeres; hind trochanter elongate, cylindrical (Ptininae)	Anobiidae	p. 427
160′.	Without combination of narrowly separated antennal insertions and no lateral carina on pronotum; other characters variable	161	
161(160′).	Pronotum with sublateral lines or grooves that extend from base to anterior margin, or at least beyond midpoint; head usually with sublateral lines extending from median margin of eye to pronotum; lateral margins of pronotum smooth, wavy, or with few obtuse angles, not acutely denticulate or serrate; head not sharply constricted to a distinct neck; body oval to elongate, subcylindrical to strongly dorsoventrally flattened	Laemophloeidae	p. 431
161′.	Pronotum without sublateral lines or grooves that extend anterad of middle; head variable; body variable, often rather convex, oval or rounded; if body flattened and pronotum with sublateral grooves, then lateral margins of pronotum sharply denticulate, anterior angles acutely projecting, or head sharply constricted behind small temples	162	
162(161′).	Mid coxal cavity open laterally	163	
162′.	Mid coxal cavity closed laterally	165	
163(162).	Antenna with 10 antennomeres, distinctly clubbed; elytra shortened, exposing all of pygidium; head abruptly constricted to form neck; 1–4 mm	Monotomidae	p. 430
163′.	Not fitting one or more of the characters in the preceding entry	164	
164(163′).	Mid and hind tarsi with same number of tarsomeres; body elongate, flattened (Figure 26–58B); head usually with distinct temples before abruptly constricted neck; fore coxa either closed behind or open; if open (Brontinae), elytra transversely flat or slightly concave between slightly to distinctly raised interstria between stria 6 and 7; elytron with scutellary striole; base of mandible with dorsal setose pit (mycangium) hidden beneath clypeus when closed; antenna filiform, with scape more than 3× length of pedicel	Silvanidae	p. 431
164′.	Hind tarsus with 1 less tarsomere than mid tarsus; other characters variable	169	

[9] Two genera of tiny (<1.3 mm) cryptophagids (*Amydropa*, Baja, California, and *Hypocoprus*, Rocky Mountain region) lack the subgenal carinae. *Hypocoprus* has the first two ventrites subequal and the pygidium exposed, whereas *Amydropa* lacks the double suture on the elytra. The other characters fit these two rare genera. *Amydropa* has greatly reduced eyes (10 facets or fewer), and *Hypocoprus* has distinct temples.

165(162′).	Body shining, oval and strongly convex; pronotum tightly embracing elytra (Figure 26–59A), pronotum laterobasally with a translucent, thin flange that slides over a smooth area on base of humeral angle of elytron, this area on elytron delimited posteriorly by a thin carina; pronotum and elytra with wide propleura and epipleura, lateral margins sharp, explanate, strongly directed ventrally so that lateral margins far below level of fore coxa and mesad of epipleural margin, dorsal surface forming an inverted U in transverse section; pretarsal claw-toothed or appendiculate	Phalacridae	p. 431
165′.	Body usually not so evenly oval; pronotum not as in preceding entry; lateral margins of pronotum and elytra laterad, not ventrad, of fore coxa and epipleura; pretarsal claws toothed only in groups with pronotum narrowed behind	166	
166(165′).	Mid and hind tarsi with same number of tarsomeres; face often with beaded lateral margins	167	
166′.	Mid tarsus with 1 more tarsomere than hind tarsus; face without beaded lateral margins	169	
167(166).	Gular sutures confluent; gena expanded anteriorly, platelike, concealing maxilla	Passandridae	p. 431
167′.	Gular sutures separate or absent; gena not so expanded	168	
168(167′).	Fore coxal cavity usually open behind; terminal maxillary palpomere narrow, elongate; if fore coxal cavity closed behind, then closed by mesal extension of hypomeron; length <3 mm and pronotum somewhat narrowed near base (*Cryptophilus*)	Languriidae	p. 431
168′.	Fore coxal cavity closed behind by lateral expansion of prosternal process; terminal maxillary palpomere often hatchet-shaped, or narrow and elongate; length 3–22 mm	Erotylidae	p. 432
169(123′, 138′, 159′, 164′, 166′).	Last visible segment of abdomen forming a terminal spine (Figure 26–63); body wedge-shaped, humpbacked; head retracted to hypognathous position; hind tibia and tarsus usually with oblique or transverse, comblike serrate ridges subapically on lateral faces	Mordellidae	p. 434
169′.	Abdomen not prolonged into a terminal spine; body otherwise variable; hind tibia and tarsus without comblike serrate ridges as in preceding entry; if similar combs are present, then they are apical	170	
170(169′).	Pretarsal claw with a ventral blade or elongate lobe beneath (reduced to a large, fused tooth ending about ⅔ length of upper blade in *Phodaga*, U.S. Southwest); head sharply or gradually constricted behind eyes to distinct neck	171	
170′.	Pretarsal claw without ventral blade or elongate lobe beneath, if claw-toothed or appendiculate, then not as in preceding entry; head constricted or not	172	
171(170).	Ventral appendage of pretarsal claw usually lobelike, membranous, occasionally bladelike and sclerotized; elytra usually meeting along suture to very near apex, which may be narrowly and separately rounded; lateral margin of pronotum absent, complete, or indicated only at base; antenna without club, or with vague to distinct club of 3 antennomeres; mid coxal cavities usually narrowly separated, occasionally contiguous; maxillae not forming sucking tube; hind wing with well-developed radial cell; if pronotal margin completely absent, antenna with at least vague indication of club in last 3 antennomeres and mid coxal cavities narrowly separated; if elytra broadly separately rounded, pronotum with lateral carina at base	Stenotrachelidae	p. 438

171′.	Ventral appendage of pretarsal claw bladelike and sclerotized; elytra usually diverging along suture before apex, broadly separately rounded (Figure 26–67A–F); pronotum lacking marginal carina laterally; antenna without club of 3 antennomeres; mid coxal cavities contiguous; maxillae usually normal, sometimes forming a sucking tube; radial cell absent in hind wing; if elytra meeting on suture to very near apex, maxillae modified into sucking tube that extends beyond mandibular apices	Meloidae	p. 438
172(170′).	Base of pronotum with marginal groove that extends laterally onto hypomeron, ending in a pit near posterior margin of coxa; pronotum narrowed posteriorly; not margined laterally; head sharply narrowed behind distinct temples to form narrow neck; elytra sparsely to densely setose	Anthicidae	p. 440
172′.	Basal groove of pronotum, if present, not ending in pit on hypomeron; pronotum margined laterally or not; elytra with or without setae, length variable	173	
173(172′).	Mid coxal cavity closed laterally	174	
173′.	Mid coxal cavity open laterally	176	
174(173).	Basal 3 ventrites connate; antenna with 11 antennomeres, submoniliform to triangular, filiform, serrate to subflabellate; cervical sclerites present	Mycteridae	p. 440
174′.	Two or no ventrites connate; antenna with 10–11 antennomeres, moniliform to capitate; cervical sclerites absent	175	
175(174′).	Prothorax with pleurosternal suture ending in a large, setose pit at anterolateral margin of fore coxal cavity; 2 basal ventrites connate; antenna with 11 antennomeres; 1.5–3.8 mm; deserts of U.S. West from Idaho to Mexican border (*Cononotus*)	Pyrochroidae	p. 440
175′.	Prothorax with or without pleurosternal suture, lacking large setose pit on anterior margin of fore coxal cavity; all ventrites usually free, or 2 basal ventrites connate (*Aegialites*); antenna with 10–11 antennomeres; length 1.5–7 mm; widespread in forests and Pacific beaches (*Aegialites*); if in deserts, antenna with 10 antennomeres (*Dacoderus*)	Salpingidae	p. 440
176(173′).	Body deep, mildly to distinctly wedge-shaped; antenna serrate, pectinate, or flabellate, often bipectinate or biflabellate; vertex often inflated and narrowed above eyes in frontal view; vertex usually extending dorsally above plane of pronotum in lateral view, vertex and pronotum at least coplanar; tarsi toothed, bifid, or pectinate; maxillary lobes sometimes styletlike, extending beyond tips of mandibles	Ripiphoridae	p. 435
176′.	Body usually not deep and wedge-shaped, if so, then antenna simple and head coplanar with or slipping under front margin of pronotum; tarsi variable; maxillary lobes not styletlike	177	
177(176′).	Pronotum lacking lateral carina	178	
177′.	Pronotum with lateral carina present, complete or incomplete	182	
178(177).	Hind coxa extending laterally to elytron or side of body, completely separating metepisternum and first ventrite	179	
178′.	Hind coxa not reaching elytron or side of body; metepisternum and first ventrite in contact laterad of hind coxa	181	
179(178).	Tarsi appearing 4-4-3 (actually 5-5-4, pseudotetramerous/pseudotrimerous); eyes coarsely faceted, appearing hairy, setae between facets as coarse, long and dense as those on front and sides of head adjacent to eyes; 1–4 mm	Aderidae	p. 440

179′.	Tarsi distinctly 5-5-4; eyes with or without setae between facets, if present, then setae not as coarse, long or obvious as on front and sides of head adjacent to the eyes; 4–21 mm	180	
180(179′).	Head prognathous, not abruptly constricted to a narrow neck, lacking distinct temples (Figure 26-66A); anterior portion of prosternum as long or longer than prosternal process	Oedemeridae	p. 438
180′.	Head distinctly declined, abruptly constricted to form narrow neck behind distinct temples; anterior portion of prosternum shorter than prosternal process (Eurygeniinae)	Anthicidae	p. 440
181(178′).	Elytra distinctly setose; eye emarginate anteriorly; penultimate tarsomere with large lobe beneath	Pyrochroidae	p. 440
181′.	Elytra glabrous; eye not emarginate; penultimate tarsomere simple (*Pytho* and *Priognathus*)	Pythidae	p. 440
182(177′).	Hind coxa extending laterally to elytra or side of body, completely separating metepisternum and first ventrite; mid tibial spurs serrate, pectinate, or pubescent	183	
182′.	Hind coxa not reaching elytra or side of body, metathorax and first ventrite at least narrowly closing hind coxal cavity laterally; mid tibial spurs variable	185	
183(182).	Head vertically narrowed behind eyes to form narrow neck, head not received into prothorax, either bulging beyond pronotal margin, or fitting closely against pronotal margin so that head in lateral view has a posterior carina or crest meeting anterior margin of pronotum	Scraptiidae	p. 441
183′.	Head gradually narrowed behind eyes, fitting into pronotum in a telescoping manner	184	
184(183′).	Tarsus without lobes on penultimate tarsomere; sutural stria deeply impressed near apex of elytra, distinctly more so than in basal half; 2 basal ventrites connate; hind tibia longer than first tarsomere; length 7–13 mm	Synchroidae	p. 437
184′.	Either tarsus with penultimate tarsomere lobed beneath, or hind tibia shorter than first tarsomere; if sutural stria deeply impressed near apex, then also impressed on basal half; length 2–20 mm	Melandryidae	p. 434
185(182′).	Fore coxal cavity closed behind; first 2 ventrites connate; body strongly rounded	Archeocrypticidae	p. 434
185′.	Fore coxal cavity open behind; ventrites connate or free; body form variable, often elongate	186	
186(185′).	Elytra with sutural and epipleural margins elevated, with strongly elevated carina running from humeral angle nearly to apex resulting in distinctly concave elytral disc; pronotum with median longitudinal elevated carina on basal third, deep transverse grooves with pits at each end on either side of carina (*Ischalia*)	Anthicidae	p. 440
186′.	Elytra and pronotum without strongly elevated carinae, elytral disc convex	187	
187(186′).	Prosternal intercoxal process incomplete or absent, not separating fore coxae	188	
187′.	Prosternal intercoxal process complete, fully separating fore coxae	189	
188(187).	Antenna filiform; terminal labial and maxillary palpomeres expanded apically; prosternum shorter than diameter of fore coxa; mid tibial spurs pubescent or serrate; tarsi lobed on penultimate tarsomeres (Osphyinae)	Melandryidae	p. 434

188'.	Antenna with long, serrate club formed of last 3 antennomeres; terminal labial and maxillary palpomeres cylindrical; prosternum as long as fore coxal diameter; mid tibial spurs smooth; tarsi not lobed (*Trimitomerus*)	Pythidae	p. 440
189(187').	Tarsi simple, lacking lobes below	190	
189'.	At least some tarsomeres distinctly lobed below	192	
190(189).	Median longitudinal line (discrimen) of metasternum short, extended from hind margin less than half total length of sclerite; mid coxa normal, convex and punctate anterior to trochanteral insertion	191	
190'.	Median longitudinal line (discrimen) of metasternum longer, extended from hind margin more than half total length of sclerite; mid coxa with unique, polished, ventral face anterior to trochanteral insertion	Tetratomidae	p. 434
191(190).	Antenna short, not reaching middle of pronotum; apical 3 antennomeres forming a distinct, rather abrupt club	Boridae	p. 440
191'.	Antenna longer, reaching base of elytron; apical antennomeres somewhat wider than basal antennomeres, but not forming abrupt club (*Sphalma*)	Pythidae	p. 440
192(189').	Antenna filiform; setae on elytra very short and indistinct, shorter than diameter of punctures; elytra uniform in color; California and Nevada (*Tydessa*)	Pyrochroidae	p. 440
192'.	Antenna strongly serrate; setae on elytra conspicuous, several times longer than diameter of punctures; elytra reddish with dark markings, a macula around scutellum and transverse band at apical third, usually joined by line along suture; south Texas	Polypriidae	p. 441
193(1').	One pretarsal claw; eye reduced to a single ommatidium	194	
193'.	Two pretarsal claws; compound eye variable: normal, reduced or with single ommatidium	195	
194(193).	Gonopore present (females)	Phengodidae	p. 423
194'.	Gonopore not present	larval Coleoptera	
195(193').	Head with median ocellus (female *Thylodrius*)	Dermestidae	p. 424
195'.	Head without median ocellus	196	
196(195').	Head prognathous; pronotum expanded anteriorly, extending over head in retracted position (*Phausis*, *Microphotus*) or head retractile into tubular prothorax (*Pterotus*); distinctly to slightly dorsoventrally flattened; antenna with 9 or fewer antennomeres; some species, possibly all, bioluminescent; widespread (females)	Lampyridae	p. 423
196'.	Head hypognathous, not retractile into prothorax; body globular-cylindrical; antenna with 11 antennomeres; not bioluminescent; Florida or near ports-of-entry (female Ripidiinae, North American females unknown)	Ripiphoridae	p. 435

SUBORDER Archostemata: Coleopterists do not agree on the relationships of the two families here considered as representing the suborder Archostemata. Most authorities consider the Cupedidae a very primitive group meriting rank as a suborder, but some (for example, Arnett 1968) would place the Micromalthidae in the suborder Polyphaga because they lack notopleural sutures. The two families in this suborder are small (only five North American species) and seldom encountered.

***Family* Cupedidae—Reticulated Beetles:** This is a small and little known group, with four genera, each with one species, occurring in the United States. All are densely scaly, with the elytra reticulate and the tarsi distinctly five-merous. The prosternum extends backward as a narrow process that fits into a groove in the mesosternum, much as in click beetles. The common species in the eastern United States, *Cupes capitatus* Fabricius, is 7–10 mm long and brownish gray. In the Rocky Mountains and the Sierra Nevada, the most common species is *Priacma serrata* (LeConte), which is gray with faint black bands across the elytra. These beetles are usually found under bark.

***Family* Micromalthidae:** This family includes a single rare species, *Micromalthus debilis* LeConte, which has been taken in several localities in the eastern United States and in British Columbia and New Mexico. The adults are 1.8–2.5 mm long, elongate and parallel-sided, dark, and shiny, with yellowish legs and antennae. The tarsi are five-merous. This insect has a remarkable life cycle, with paedogenetic larvae. The larvae can reproduce parthenogenetically (both oviparously and viviparously). These beetles have been found in decaying logs, principally oak and chestnut.

SUBORDER Myxophaga: The suborder contains two small families of tiny beetles that live in water or wet places and apparently feed on filamentous algae (to which the suborder name refers). The Myxophaga are distinguished by the character of the wings and mouthparts and by the presence of notopleural sutures. All have three-merous tarsi and clubbed antennae. The two families of Myxophaga are usually keyed out on the basis of their having notopleural sutures (from couplet 2 in the key). The Microsporidae are very tiny, and the notopleural sutures may be very difficult to see, so we have also keyed out this family from couplet 2′ (notopleural sutures lacking).

***Family* Microsporidae—Minute Bog Beetles:** The microsporids are tiny (0.5–0.75 mm long), oval, convex, shining, blackish beetles with a large, prominent head and capitate antennae that are found in mud and under stones near water, among roots of plants, and in moss in boggy places. They differ from other similarly shaped beetles found in these situations in having three-merous tarsi and in the character of the abdomen, in which the first ventrite is a triangular piece between the hind coxae, the second a narrow transverse band, and the third occupying most of the lower surface of the abdomen. The group is represented in the United States by three species that occur in the eastern states, Texas, Arizona, southern California, and Washington.

***Family* Hydroscaphidae—Skiff Beetles:** The skiff beetles are about 1.5 mm long, with three-merous tarsi and short elytra, and are similar in general appearance to rove beetles. The antennae are eight-merous, with a club composed of one antennomere. They live in the filamentous algae growing on rocks in streams. The group is represented in the United States by a single species, *Hydroscapha natans* LeConte, which occurs in southern California, southern Nevada, and Arizona.

SUBORDER Adephaga: The members of the suborder Adephaga have the hind coxae dividing the first visible abdominal sternum (Figure 26–12A). The posterior margin of this sternum does not extend completely across the abdomen, but is interrupted by the hind coxae. Nearly all the Adephaga have filiform antennae and 5-5-5 tarsi; they have notopleural sutures; and most are predaceous.

***Family* Rhysodidae—Wrinkled Bark Beetles:** The members of this group are slender, brownish beetles 5.5 to 7.5 mm long with three fairly deep longitudinal grooves on the pronotum and with moniliform antennae (Figure 26–14). The pronotal grooves are complete in *Omoglymmius*, but are present on only about the posterior third of the pronotum in *Clinidium*. These beetles are usually found under the bark of decaying beech, ash, elm, or pine. Eight species occur in the United States, one of each genus in the West, and the others in the East.

***Family* Carabidae (including Cicindelidae)—Ground Beetles and Tiger Beetles:** This is the third largest family of beetles in North America (the Staphylinidae and Curculionidae are larger), with more than 2,600 species grouped into 189 genera in North America. Its members exhibit considerable variation in size, shape, and color. Most species are dark, shiny, and somewhat flattened, with striate elytra (Figure 26–15).

Ground beetles are commonly found under stones, logs, leaves, bark, or debris or running about on the ground. When disturbed, they run rapidly, but seldom fly. Most species hide during the day and feed at night. Many are attracted to lights. Nearly all are predaceous on other insects, and many are very beneficial. The members of a few genera (for example, *Scaphinotus*, Figure 26–15B) feed on snails. The larvae are also predaceous and live in burrows in the soil, under bark, or in debris.

The largest and most brilliantly colored ground beetles belong to the genus *Calosoma*; these are often

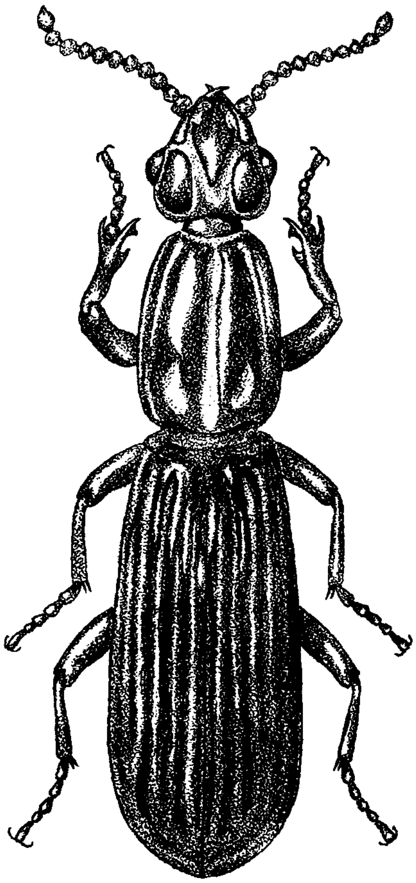

Figure 26–14 A wrinkled bark beetle, *Clinidium sculptilis* Newman, 14×. (Courtesy of Arnett.)

called "caterpillar hunters," because they feed chiefly on caterpillars, particularly those that attack trees and shrubs. Most of these beetles are 25 mm or more in length. When handled, they give off a very disagreeable odor. *Calosoma sycophanta* L., a brilliant greenish beetle with a dark-blue pronotum, was introduced from Europe to aid in the control of the gypsy moth. These beetles are attracted to lights.

The species in the genus *Brachinus* are called "bombardier beetles" because they eject from the anus what looks like a puff of smoke. This glandular fluid is ejected with a popping sound and vaporizes into a cloud when it comes in contact with the air. The discharge of some species may irritate tender skin. This apparently serves as a means both of protection and of offense.

A few of the carabids are plant feeders. Adults of *Stenolophus lecontei* (Chaudoir), the seed-corn beetle, and *Clivina impressifrons* LeConte, the slender seed-corn beetle, sometimes attack corn seeds in the soil and prevent them from sprouting. This behavior occasionally causes considerable damage, especially during cold springs when germination is delayed.

The members of the genus *Omophron*, called *round sand beetles* (and formerly placed in a separate family, the Omophronidae), differ from other carabids in having the scutellum concealed. They are small (5–8 mm long), oval convex beetles that live in wet sand along the shores of lakes and streams. They can be found running over the sand or burrowing in it (particularly under stones) and may occasionally be found running over the surface of the water. They run when disturbed and seldom fly. Adults and larvae are predaceous, but the larvae occasionally feed on seedlings of crops planted in moist soil.

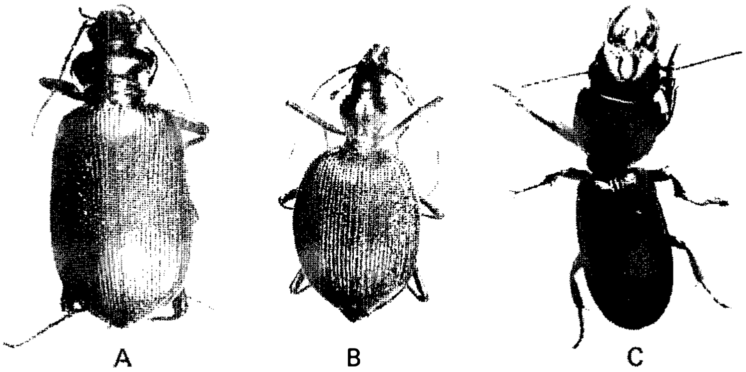

Figure 26–15 Ground beetles. A, *Calosoma scrutator* (Fabricius); B, *Scaphinotus guyoti* (LeConte); C, *Scarites subterraneus* (Fabricius). All figures slightly enlarged. (C, courtesy of the Illinois Natural History Survey.)

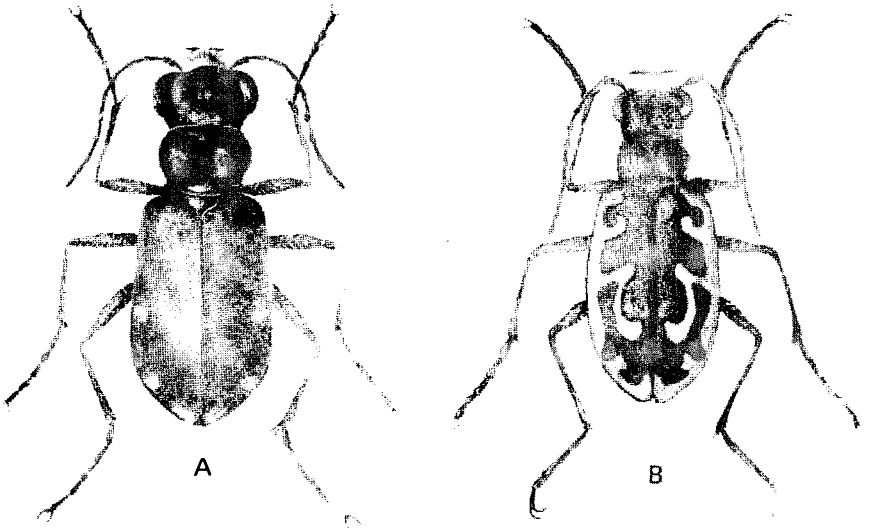

Figure 26–16 Tiger beetles. A, *Cicindela sexguttata* (Fabricius); B, *C. hirticollis* Say, 3×.

Tiger beetles (subfamily Cicindelinae) are a favorite of beetle collectors because of their bright colors and the challenge of capturing them. Some workers regard them as a family separate from the Carabidae. There are 111 species in four genera of tiger beetles in North America, most belonging to the genus *Cicindela*.

Adult tiger beetles are usually metallic or iridescent and often have a definite color pattern. They can usually be recognized by their characteristic shape (Figure 26–16), and most are 10–20 mm long.

Most tiger beetles are active, usually brightly colored insects found in open, sunny situations. They are often common on sandy beaches. They can run or fly rapidly and are very wary and difficult to approach. They take flight quickly, sometimes after running a few feet, and usually alight some distance away facing the pursuer. They are predaceous and feed on a variety of small insects, which they capture with their long, sicklelike mandibles. When handled, they sometimes administer a painful bite.

The larvae are predaceous and live in vertical burrows in the soil in dry paths or fields or in sandy beaches. They prop themselves at the entrance of their burrow, with the traplike jaws wide apart, waiting to capture some passing insect. The larva has hooks on the fifth abdominal tergum, with which it can anchor itself in its burrow and thus avoid being pulled out when it captures large prey. After subduing the prey, the larva drags it to the bottom of the burrow, often 0.3 m underground, and eats it.

Family **Gyrinidae—Whirligig Beetles:** The gyrinids are oval black beetles that are commonly seen swimming in endless gyrations on the surface of ponds and quiet streams. They are equally at home on the surface of the water or beneath it. They are extremely rapid swimmers, swimming principally by means of the strongly flattened middle and hind legs, which move in synchrony (as in Dytiscidae). The front legs are elongate and slender (Figure 26–17). These insects are peculiar in having each compound eye divided. They have a pair of compound eyes on the upper surface of the head and another pair on the ventral surface (Figure 26–17C). The antennae are very short and somewhat clubbed and their third antennomere is greatly expanded and somewhat earlike (Figure 26–5E). The two basal abdominal sterna are fused, and the suture separating them is indistinct.

Adult whirligig beetles are principally scavengers, feeding chiefly on insects that fall onto the surface of the water. The larvae (Figure 26–18A) are predaceous, feeding on a variety of small aquatic animals, and are often cannibalistic. Many adults give off a characteristic fruity odor when handled. The adults are often gregarious, forming large swarms on the surface of the water.

The eggs of whirligig beetles are laid in clusters or rows on the undersides of the leaves of aquatic plants, particularly water lilies and pondweed. Pupation occurs in mud cells on the shore or on aquatic plants.

Most of the 56 North American species of whirligig beetles belong to the genera *Gyrinus* and *Dineutus*. The species of *Dineutus* are 8.5–15.5 mm long, and the scutellum is hidden (Figure 26–17A).

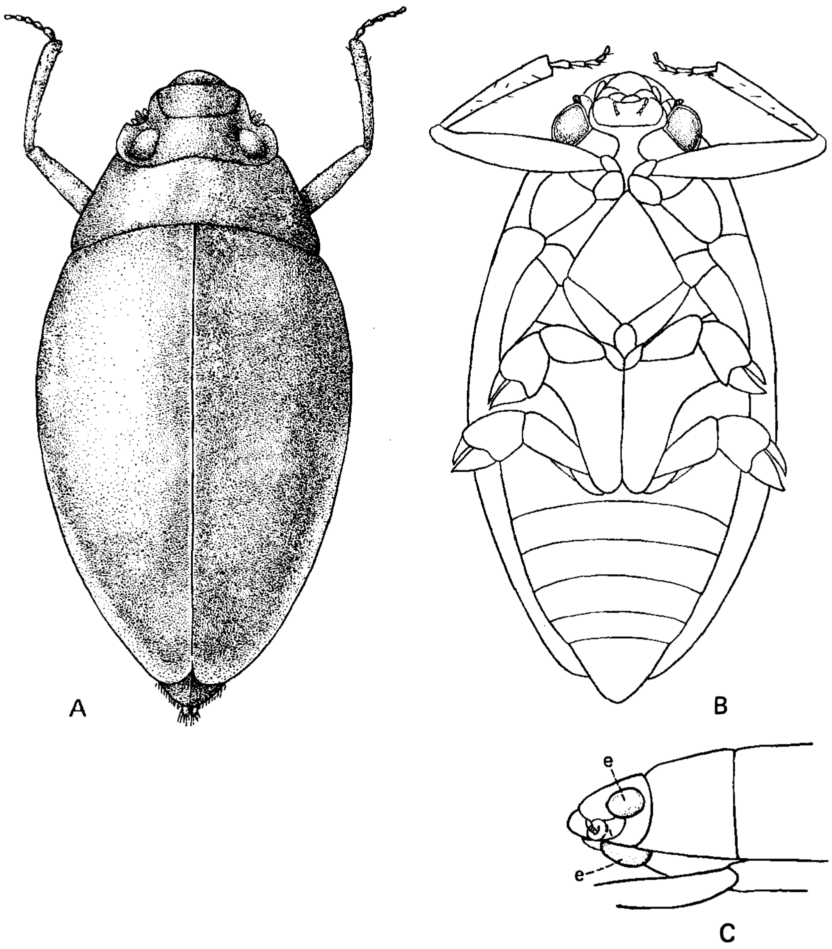

Figure 26–17 A whirligig beetle, *Dineutus americanus* (Say), 7×. A, dorsal view; B, ventral view; C, lateral view.

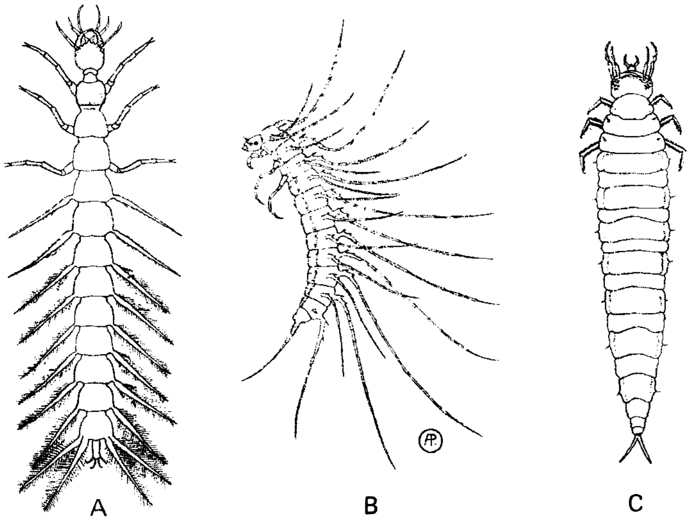

Figure 26–18 Larvae of aquatic beetles. A, *Dineutus* (Gyrinidae); B, *Peltodytes* (Haliplidae), lateral view; C, *Hydrophilus triangularis* (Say) (Hydrophilidae). (Courtesy of Peterson. Reprinted by permission.)

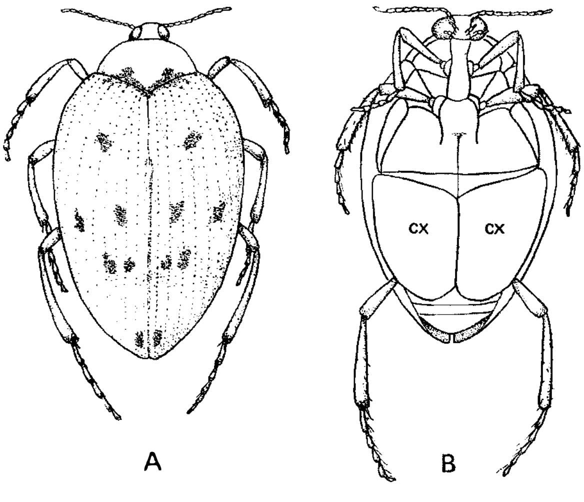

Figure 26–19 A crawling water beetle, *Peltodytes edentulus* (LeConte), 11×. A, dorsal view; B, ventral view. *cx*, hind coxa.

Family **Haliplidae—Crawling Water Beetles:** The haliplids are small, oval, convex beetles 2.5–4.5 mm long, that live in or near water. They are usually yellowish or brownish with black spots (Figure 26–19A) and can be distinguished from similar aquatic beetles by their very large and platelike hind coxae (Figure 26–19B). They are fairly common in and about ponds, swimming or moving about rather slowly. They frequently live in masses of vegetation on or near the surface of the water. The adults feed chiefly on algae and other plant materials. The larvae (Figure 26–18B) are predaceous. There are 63 species of Haliplidae in North America. The two common eastern genera in this group can be separated by the presence or absence of two black spots at the base of the pronotum. These spots are present in *Peltodytes* (Figure 26–19A) and absent in *Haliplus*.

Family **Noteridae—Burrowing Water Beetles:** These beetles are very similar to the dytiscids, but have the scutellum hidden and have two equal claws on the hind tarsus. They are broadly oval, smooth, brownish to black beetles, 1.2 to 5.5 mm long, and are similar to the dytiscids in habits. The common name of this group refers to the larvae, which burrow into the mud around the roots of aquatic plants and apparently feed on algae. There are 14 species in the United States and Canada.

Family **Amphizoidae—Trout-Stream Beetles:** This family contains six species in the genus *Amphizoa*, three occurring in western North America and the other three in China. These beetles are oval, dark-colored, and 11.0–15.5 in length. Adults and larvae of most species live in the cold water of mountain streams, where they crawl about on submerged objects or on driftwood. One species occurring near Seattle lives in relatively warm, quiet water. The larvae do not have gills and must obtain oxygen at the water surface. They frequently crawl out of the water onto twigs or floating objects. When dislodged, they float until they can grasp another object, as they apparently do not swim. The adults swim very little and often run about on stream shores at night. Both adults and larvae are predaceous, feeding largely (if not entirely) on stonefly nymphs.

Family **Dytiscidae—Predaceous Diving Beetles:** This is a large group of aquatic beetles (more than 500 species in 52 genera in North America) that are usually very common in ponds and quiet streams. The body is smooth, oval, and very hard, and the hind legs are flattened and fringed with long hairs to form excellent paddles. These beetles obtain air at the surface of the water, but can remain submerged for long periods because they carry air in a chamber under the elytra. They often hang head downward from the surface of the water. These insects may leave the water at night and fly to lights.

The dytiscids are very similar to another group of beetles common in fresh water, the Hydrophilidae. The adults of these two groups may be distinguished by the structure of the antennae and the maxillary palps and sometimes by the structure of the metasternum. The dytiscids have long, filiform antennae and very short maxillary palps (Figure 26–20), whereas the antennae of the hydrophilids are short and clubbed, and the maxillary palps are nearly always as long as or longer than the antennae (Figure 26–22). The metasternum in many hydrophilids is prolonged posteriorly into a long spine (Figure 26–22B). An excellent field character for separating these two groups is their method of swimming. The dytiscids move the hind legs together, like a pair of oars, whereas the hydrophilids move the hind legs alternately, as though they were running through the water.

Both adults and larvae of the dytiscids are highly predaceous and feed on a variety of small aquatic animals, including small fish. The larvae (Figure 26–21) are often called *water tigers*. They have long, sicklelike jaws, which are hollow, and when they attack prey they suck out its body fluids through the channels in the jaws. These larvae are very active and do not hesitate to attack an animal much larger than themselves.

Adult dytiscids vary in length from 1.2 to 40 mm. Most are brownish, blackish, or greenish. The males of some species (Figure 26–20B) have peculiar front tarsi bearing large suction discs used in holding the smooth, slick elytra of the female for mating. Some of the larger species have a pale yellow band along the lateral mar-

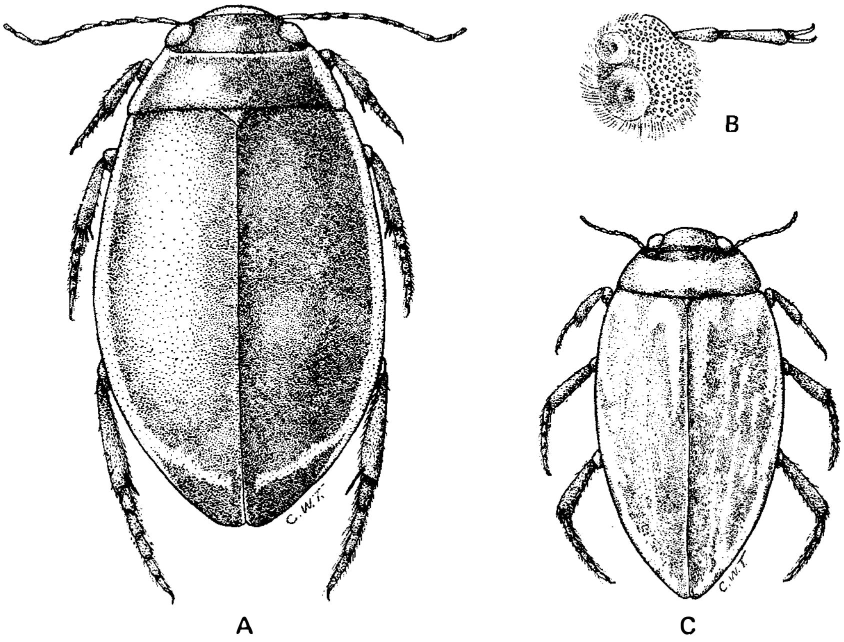

Figure 26–20 Predaceous diving beetles. A, *Dytiscus verticalis* (Say), female, 2×; B, same, front tarsus of male; C, *Coptotomus interrogatus* (Fabricius), 7×.

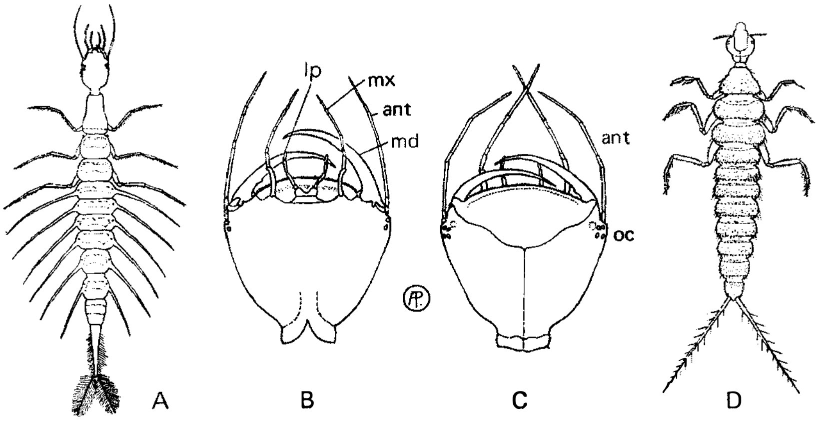

Figure 26–21 Larvae of Dytiscidae. A, *Coptotomus*; B, head of *Dytiscus*, ventral view; C, same, dorsal view; D, *Hydroporus*. *ant*, antenna; *lp*, labial palp; *md*, mandible; *mx*, maxilla; *oc*, ocelli. (Courtesy of Peterson. Reprinted by permission.)

gins of the pronotum and elytra (Figure 26–20A). A few members of this group have tarsi in a 4-4-5 pattern.

SUBORDER Polyphaga: The members of this suborder differ from most other beetles in that the first visible abdominal sternum is not divided by the hind coxae, and its posterior margin extends completely across the abdomen. The hind trochanters are usually small, not large, and are offset toward the midline as in the Adephaga (Figure 26–12B), and notopleural sutures are lacking. This suborder includes the remaining families of beetles, which vary greatly in the form of the antennae, the tarsal formula, and other characters.

***Family* Hydrophilidae—Water Scavenger Beetles:** The hydrophilids are oval, somewhat convex beetles that can be recognized by the short, clubbed antennae and the long maxillary palps (Figure 26–22). Most species are aquatic and are very similar in general appearance to the Dytiscidae. The aquatic species are generally black, and they vary in length from a few millimeters up to about 40 mm. The metasternum in some species is prolonged posteriorly as a sharp spine (Figure 26–22B). This spine may be jabbed into the fingers of a person who is careless in handling one of these insects.

The water scavenger beetles differ somewhat from the dytiscids in habits. They rarely hang head downward from the surface of the water, as the dytiscids frequently do, and they carry air with them below the wa-

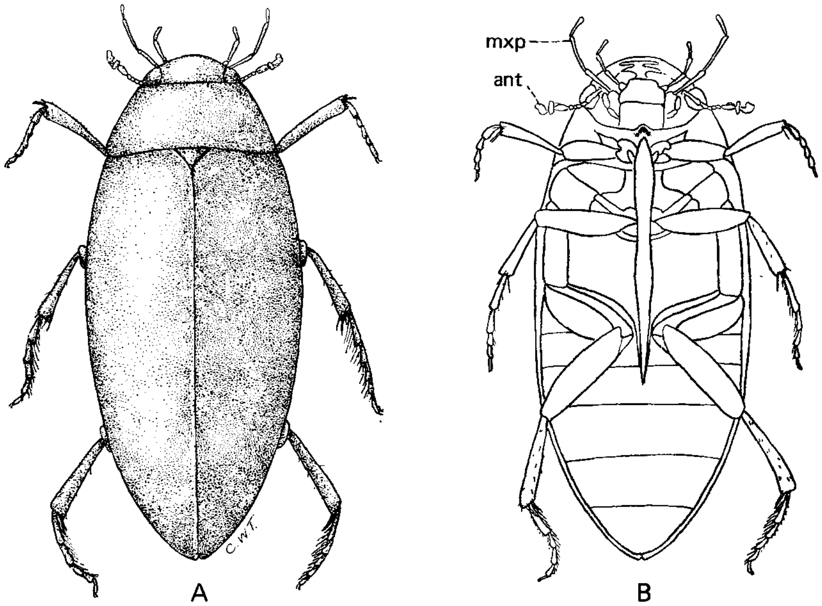

Figure 26–22 A water scavenger beetle, *Hydrophilus triangularis* Say. A, dorsal view; B, ventral view. *ant*, antenna; *mxp*, maxillary palp.

ter in a silvery film over the ventral side of the body. In swimming, the hydrophilids move opposite legs alternately, whereas the dytiscids move opposite legs simultaneously, like a frog. The adults are principally scavengers, as the common name implies, but the larvae are usually predaceous. The larvae of the water scavenger beetles (Figure 26–18C) differ from those of the predaceous diving beetles in that they have only a single pretarsal claw (dytiscid larvae have two), and the mandibles are usually toothed. The larvae are voracious and feed on all sorts of aquatic animals.

The hydrophilids (284 North American species) are common insects in ponds and quiet streams. A large and common species, *Hydrophilus triangularis* Say, is shining black and about 40 mm long (Figure 26–22). Most hydrophilids are aquatic, but a few (subfamily Sphaeridiinae) are terrestrial and live in dung. These differ from the aquatic hydrophilids in having the first tarsomere of the hind tarsi rather long, and the maxillary palps are usually shorter than the antennae. The most common dung-inhabiting species is *Sphaeridium scarabaeoides* (L.), which has a faint red spot and a fainter yellow spot on each elytron. Some of the aquatic species are attracted to lights at night. The aquatic species lay their eggs in silken cases, which are usually attached to aquatic plants. The full-grown larvae leave the water to pupate in earthen cells underground.

Family **Sphaeritidae—False Clown Beetles:** This group is represented in North America by a single species that lives in carrion, manure, and decaying fungi from Alaska to northern Idaho and California. This species, *Sphaerites politus* Mannerheim, is 3.5–5.5 mm long and black with a metallic bluish luster. It is very similar to some of the hister beetles, but the antennae are not elbowed, the tibiae are less expanded and lack teeth externally, and only the last abdominal segment is exposed beyond the elytra.

Family **Histeridae—Clown Beetles, Hister Beetles:** Hister beetles are small (0.5–10.0 mm long), broadly oval beetles that are usually shining black. The elytra are cut off square at the apex, exposing one or two apical abdominal segments (Figure 26–23A). The antennae (Figure 26–51) are elbowed and clubbed. The tib-

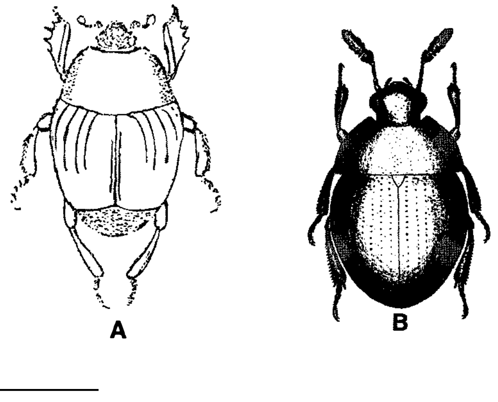

Figure 26–23 A, a hister beetle, *Geomyzaprinus goffi* (Ross), 6×; B, a round fungus beetle, *Anisotoma globosa* Hatch, 15×. (A, courtesy of Ross and the Entomological Society of America; B, courtesy of Wheeler and Blackwell Scientific Publications.)

iae are dilated, and the anterior ones are usually toothed or spined. Hister beetles are generally found in or near decaying organic matter such as dung, fungi, and carrion, but are apparently predaceous on other small insects living in these materials. Some species, which are very flat, live under the loose bark of stumps or logs. A few live in the nests of ants or termites. A few species are elongate and cylindrical; these live in the galleries of wood-boring insects. When disturbed, the hister beetles usually draw in their legs and antennae and become motionless. The appendages fit so snugly into shallow grooves on the ventral side of the body that it is often difficult to see them, even with considerable magnification. Around 435 species occur in the United States and Canada.

Family **Hydraenidae—Minute Moss Beetles:** These beetles are similar to the hydrophilids but differ in having six or seven abdominal sterna (only five in the Hydrophilidae). They are elongate or oval, dark-colored beetles, 1.2 to 1.7 mm long, and live in matted vegetation along stream margins, in wet moss, and along the seashore. Both larvae and adults feed on algae. There are 95 species in six genera in North America.

Family **Ptiliidae—Feather-Winged Beetles:** This family includes some of the smallest beetles known. Few exceed 1 mm, and many are less than 0.5 mm long. The body is oval, the hind wings bear a long fringe of hairs that often extends out from beneath the elytra, and the antennae bear whorls of long hairs. These beetles live in rotting wood, dung, and leaf litter and feed chiefly on fungus spores. In North America, 27 genera and nearly 120 species are known.

This family includes the horseshoe crab beetles, formerly placed in the Limulodidae, which are usually a millimeter or less in length and are somewhat similar to horseshoe crabs in general appearance. They are oval in shape, with the elytra short and the abdomen somewhat tapering, and yellowish to brownish. Hind wings and compound eyes are absent. These beetles are found in ant nests, where they usually ride on the ants, feeding on exudations from their bodies. This group is a small one (four species in the United States), but is widely distributed.

Family **Agyrtidae—Primitive Carrion Beetles:** This is a small group (11 North American species) formerly included in the Silphidae. These beetles are 4–14 mm long, oblong to elongate in shape, slightly flattened, and glabrous. They are found in decaying animal or vegetable matter. There is 1 eastern species; the other 10 occur in the Pacific Coast states.

Family **Leiodidae—Round Fungus Beetles, Mammal-Nest Beetles, Beaver Parasites:** The leiodids, with about 324 species in 30 genera in North America, are a variable group that was formerly divided into at least two families. The Leiodinae are convex, shiny, oval beetles, 1.5 to 6.5 mm long, and brown to black (Figure 26–23B). Many species when disturbed tuck the head and prothorax under the body and roll into a ball, thus concealing all the appendages. These beetles live in fungi, under bark, in decaying wood, and in similar places. The Catopinae (formerly placed in the family Leptodiridae) are elongate-oval, somewhat flattened, brownish to black, pubescent, and 2–5 mm long. They often have faint cross striations on the elytra and pronotum, and most have the eighth antennomere shorter and smaller in diameter than the seventh and ninth antennomeres. Most of these beetles live in carrion, but some are found in fungi, some feed on slime molds, and others live in ant nests. The highly modified *Glaciacavicola bathyscoides* Westcott is known only from Idaho ice caves.

The mammal-nest beetles and beaver parasites (formerly classified separately as the Leptinidae and Platypsyllidae) are brownish, oblong-oval, louselike beetles, 2–5 mm long, with the eyes reduced or absent. The species of *Leptinus* (three in North America) live in the nests and fur of mice, shrews, and moles and occasionally in the nests of ground-nesting Hymenoptera. The species of *Leptinillus* (two in North America) live in the nests and fur of beavers, one species on the common beaver (*Castor*) and the other on the mountain beaver (*Aplodontia*). The single species of *Platypsylla*, *P. castoris* Ritsema, is an ectoparasite of the common beaver.

Family **Scydmaenidae—Antlike Stone Beetles:** The members of this group are antlike in shape (Figure 26–24B), long-legged, brownish, somewhat hairy beetles, 1–5 mm long. The antennae are slightly clavate, and the femora are often clavate (Figure 26–24B). They live under stones, in moss and leaf litter, and in ant nests. These beetles are secretive in habit, but sometimes fly about in numbers at twilight. There are 217 species in North America.

Family **Silphidae—Carrion Beetles:** The common species in this group are relatively large and often brightly colored insects that live around the bodies of dead animals. The body is soft and somewhat flattened, the antennae are clubbed (clavate or capitate), and the tarsi are five-merous. Silphids range in length from 3 to 35 mm, but most species are over 10 mm.

Two common genera in this group are *Silpha* and *Nicrophorus* (=*Necrophorus*). In *Silpha* (Figure 26–25A) the body is broadly oval and flattened, 10–24 mm long, and the elytra are rounded or acute at the apex and almost cover the abdomen. In some species (for example, *S. americana* L.), the pronotum is yellowish with a black spot in the center. In *Nicrophorus* (Figure 26–25B), the body is more elongate, the elytra are short and truncate apically, and most species are red and black. The beetles of the genus *Nicrophorus* are often known as "burying beetles." They excavate beneath the dead body of a mouse or other small animal, and the body sinks into the ground. These beetles are remarkably strong. A pair may move an animal as large as a rat several feet to get it to a suitable spot for burying. After the body is buried, the eggs are laid on it. Both adults and larvae feed on carrion and are usually found beneath the bodies of dead animals.

Other species of silphids live in various types of decaying animal matter. Some live in fungi, a few live in ant nests, and at least one species, *Silpha bituberosa* LeConte, feeds on plant materials. A few are predaceous on maggots and other animals that live in decaying organic matter. In some species (for example, *Nicrophorus*), the newly hatched larvae are fed carrion regurgitated by the parent beetles. In the United States and Canada, there are 30 species in eight genera.

***Family* Staphylinidae—Rove Beetles:** The rove beetles (Figures 26–24A, 26–26, 26–27) are slender and elongate and can usually be recognized by the very short elytra. The elytra are usually not much longer than their combined width, and a considerable portion of the abdomen is exposed beyond their apices (Figure 26–26). There are six or seven visible abdominal sterna, which

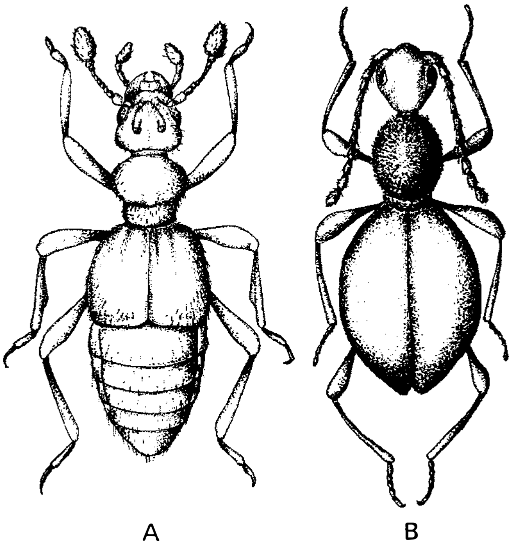

Figure 26–24 A, A short-winged mold beetle, *Trimiomelba dubia* (LeConte) (Staphylinidae, Pselaphinae), 30×; B, an antlike stone beetle, *Euconnus clavipes* (Say) (Scydmaenidae), 18×, (Redrawn from Arnett.)

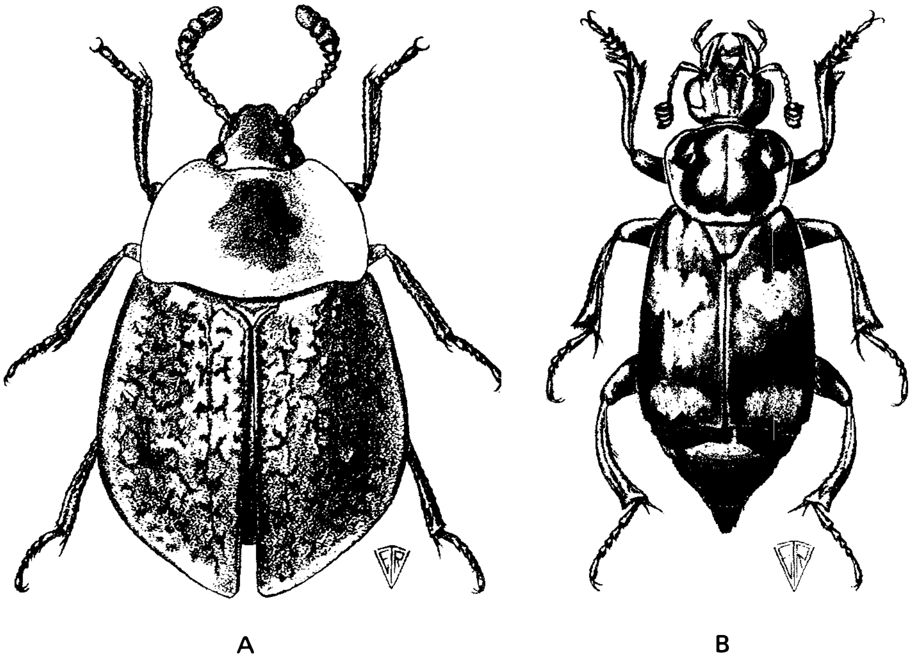

Figure 26–25 Carrion beetles. A, *Silpha americana* L.; B, *Nicrophorus sayi* Laporte; 3×. (Courtesy of Arnett.)

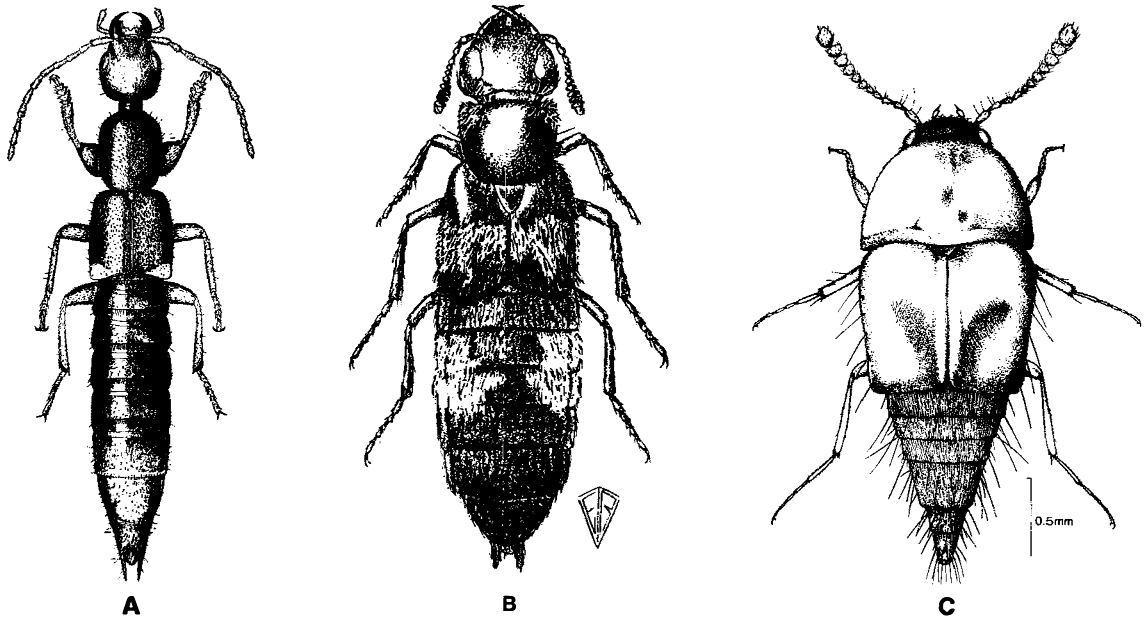

Figure 26–26 Rove beetles. A, *Lathrobium angulare* LeConte, 8×; B, *Creophilus maxillosus* (L.), 4×; C, *Sepedophilus scriptus* (Horn), 7½×. (A, courtesy of Watrous; B, courtesy of Campbell.)

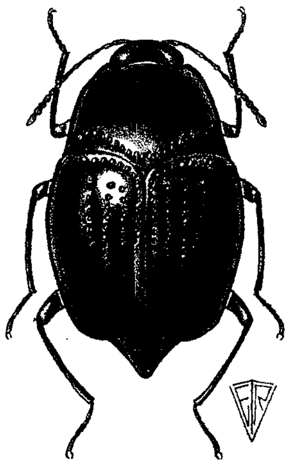

Figure 26–27 A rove beetle, *Scaphidium quadriguttatum piceum* Melsheimer, 7×. (Courtesy of Arnett.)

differentiate them from short-winged Nitidulidae (such as *Conotelus*). The hind wings are well developed and, at rest, are folded under the short elytra. Rove beetles are active insects and run or fly rapidly. When running, they frequently raise the tip of the abdomen, much as scorpions do. The mandibles are very long, slender, and sharp and usually cross in front of the head. Some of the larger rove beetles can inflict a painful bite when handled. Most of these beetles are black or brown. They vary considerably in size, but the largest are about 25 mm long.

This is one of the two largest families of beetles, with 4,153 North American species. These beetles live in a variety of habitats, but are probably most often seen about decaying materials, particularly dung or carrion. They also live under stones and other objects on the ground, along the shores of streams and the seashore, in fungi and leaf litter, and in the nests of birds, mammals, ants, and termites. Most species appear to be predaceous. The larvae usually live in the same places and feed on the same things as the adults. A few are parasites of other insects.

The short-winged mold beetles (subfamily Pselaphinae) consists of small yellowish or brownish beetles, 0.5 to 5.5 mm long (mostly about 1.5), and most are found under stones and logs, in rotting wood, and in moss. A few live in ant, termite, and mammal nests. These beetles have short, truncate elytra and resemble rove beetles, but have only three tarsomeres (most rove beetles have more), the pronotum is narrower than the elytra, and the antennae are usually abruptly clubbed

(Figure 26–24A). This group, sometimes considered a separate family, is large, with 710 species in North America. The members of one tribe of pselaphines, the Clavigerini, are peculiar in having two-merous antennae and tarsi with only one claw. These beetles live in ant nests, where the ants "milk" them for a secretion on which the ants feed. Most pselaphines are thought to be predators.

The subfamily Dasycerinae includes the genus *Dasycerus*, which was formerly placed in the family Latridiidae. It includes only four species in North America, three eastern and one western. These beetles differ from the Latridiidae in having the front coxal cavities open behind and the front coxae contiguous. Their habits are similar to those of the Latridiidae.

Family **Lucanidae—Stag Beetles:** The lucanids are sometimes called "pinchingbugs" because of the large mandibles of the males (Figure 26–28A). In some males the mandibles are half as long as the body or longer and are branched like the antlers of a stag (hence the name "stag beetles"). Stag beetles are closely related to the Scarabaeidae, but the terminal antennomeres (Figure 26–6E) cannot be held tightly together as in the scarabs and related families (Figure 26–6C,D,G). North American stag beetles vary in length from about 10–60 mm. Most of the larger ones are 25–40 mm long. There are 24 species in eight genera in the United States and Canada.

These insects are usually found in woods, but some species live on sandy beaches. The adults are often attracted to lights at night. The larvae are found in decaying wood and are similar to the white grubs found in grassy soil. They feed on liquid from the decaying wood.

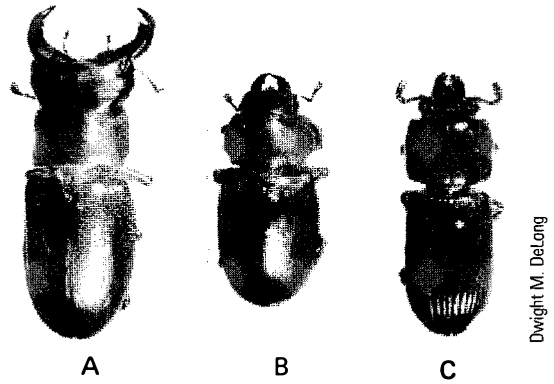

Figure 26–28 A, male, and B, female, of a stag beetle, *Pseudolucanus capreolus* (L.); C, a bessbug, *Odontotaenius disjunctus* (Illiger). About natural size.

Family **Passalidae—Bess Beetles:** These beetles have a variety of names: "bessbugs," "bessiebugs," "betsy beetles," "patent-leather beetles," and "horned passalus beetles." This family is closely related to the Lucanidae, but differs in that the mentum of the labium is deeply notched. Four species occur in the United States. The most widespread eastern species, *Odontotaenius disjunctus* (Illiger) (Figure 26–28C), is a shining black beetle, 32–36 mm long, with longitudinal grooves in the elytra and a characteristic horn on the head (Figure 26–13B). *Odontotaenius floridanus* Schuster is found in Florida. Two western species of the family were found in Arizona, but have not been observed there for many years.

The passalids are somewhat social, and their colonies live in galleries in decaying logs. The adults can produce a squeaking sound by rubbing roughened areas on the underside of the wings across similar areas on the dorsal side of the abdomen. The larvae also stridulate. This sound is produced when the insect is disturbed. Normally, however, it probably serves as a means of communication. The adults prepare food (decaying wood) with their salivary secretions and feed it to the young.

Family **Diphyllostomatidae:** This small family consists of three species of *Diphyllostoma*, all from California. They were originally described in the family Lucanidae and differ from all other scarabaeoids in having seven abdominal ventrites, exposed protrochantin, and no tibial spurs. The legs and body are very setose. Females differ from males in having reduced eyes and vestigial wings. The larvae are undescribed, and little is known of their ecology and habits.

Family **Ceratocanthidae:** These beetles are round, blackish, and 5–6 mm long, with the middle and hind tibiae greatly dilated and bearing rows of spines along their entire length. When disturbed, these beetles draw in their legs and antennae and form a hemispherical mass, and in this position they remain motionless. They live under bark, in rotten logs and stumps, and occasionally on flowers. Three species occur in the United States: two species of *Germarostres*, which are widely distributed throughout the East, and *Acanthocerus aeneus* MacLeay, which occurs in the Southeast.

Family **Glaphyridae:** The members of this group are elongate and brownish and have a very hairy body. The elytra are short, exposing two or three abdominal terga. They taper posteriorly and are separated at the apex. These beetles are 13–18 mm long. The North American species belong to the genus *Lichnanthe*. Some occur in the Northeast and some in the West. All are quite rare.

Family **Pleocomidae—Rain Beetles:** These beetles are so called because the males fly and seek mates during the fall rains. The females are wingless. The 26 species and 6 subspecies are western in distribution and relatively rare. The larvae live in the soil and feed on the roots of trees and grasses. The adults live in burrows in the ground, usually coming out only at dusk or after a rain. The members of the genus *Pleocoma* are stout-bodied, relatively large (about 25 mm long), and rather pubescent. The burrows of *P. fimbriata* LeConte are about 25 mm in diameter and up to 0.6 m in depth.

***Family* Geotrupidae—Earth-Boring Dung Beetles:** These beetles are very similar to some of the other dung-feeding scarabs, but have 11-merous antennae. They are stout-bodied, convex, oval beetles that are black or dark brown (Figure 26–29A). The elytra are usually grooved or striate, the tarsi are long and slender, and the front tibiae are broadened and toothed or scalloped on the outer edges. The elytra completely cover the abdomen. These beetles vary in length from 5 to 25 mm and are found beneath cow dung, horse manure, or carrion. Some live in logs or decaying fungi. The larvae live in or beneath dung or carrion. They feed on this material and hence are of value as scavengers. Twelve genera and 28 species of Geotrupidae occur in the Nearctic region.

***Family* Ochodaeidae:** These beetles may be recognized from other scarabaeoids in having the longer apical spur of the hind tibia pectinate along one edge. There are 35 species in four genera in North America, and they range in length from 3 to 10 mm. Little is known of the biology, except that large numbers are sometimes attracted to light. One species, *Ochodaeus musculus* (Say), a reddish-brown oval beetle, 5–6 mm long, with striate elytra, occurs in the northern states.

***Family* Hybosoridae:** These beetles may be distinguished from other scarabaeoids by the prominent mandibles and labrum, the 10-merous antennae with a 3-merous club in which the basal antennomere of the club is hollowed out to receive the two apical antennomeres. Two species are known from the United States, *Hybosorus illigeri* Reiche, which was introduced from Europe in the 1840s, and *Pachyplectrus laevis* (LeConte), a quite rare species that is found in Arizona and southern California.

***Family* Glaresidae:** This is a small family, having 15 species in the genus *Glaresis* in North America. They were formerly placed in the family Trogidae, but differ from them in having the eyes divided by a canthus and the hind femur and tibia enlarged and covering most of the abdomen. Adults live in dry, sandy areas and are attracted to light. These beetles are small (2.5–6.0 mm long).

***Family* Trogidae—Skin Beetles:** The members of this group have the dorsal surface of the body very rough. The second antennomere arises before the tip of the first instead of from its apex (Figure 26–6G). These beetles are oblong, convex, dark brown (and often covered with dirt), and shaped much like june beetles (Figure 26–29B). They are usually found on old, dry animal carcasses, where they feed on the hide, feathers, hair, or dried tissues on the bones. They represent one of the last stages in the succession of insects living in animal carcasses. Some species live in owl pellets, beneath bark, or on roots. When disturbed, these beetles draw in their legs and lie motionless, resembling dirt or rubbish, and thus are often overlooked. They overwinter as adults beneath leaves and in debris. Two genera, *Trox* with 25 species, and *Omorgus*, with 16 species, are generally distributed in the United States and Canada.

***Family* Scarabaeidae—Scarab Beetles:** This group contains about 1,400 North American species, and its members vary greatly in size, color, and habits. The scarabs are heavy-bodied, oval or elongate, usually convex beetles, with the tarsi 5-merous (rarely, the front tarsi are absent) and the antennae 8- to 11-merous and lamellate. The last three (rarely more) of the antennomeres are expanded into platelike structures that

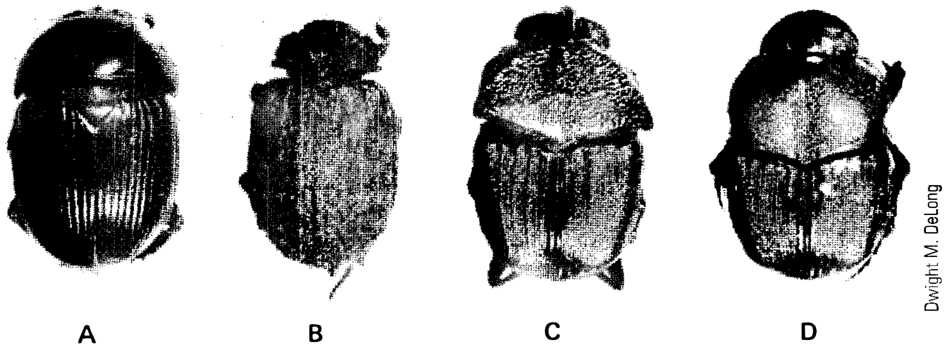

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Figure 26–29 Scarabaeoid beetles. A, an earth-boring dung beetle, *Geotrupes splendidus* (Fabricius) (Geotrupidae); B, a skin beetle, *Trox scabrosus* Beauvois (Trogidae); C, male, and D, female, of a dung beetle, *Phanaeus vindex* MacLachlan (Scarabaeidae); 1½×.

may be spread apart (Figure 26–6C) or united to form a compact terminal club (Figure 26–6D). The front tibiae are more or less dilated, with the outer edge toothed or scalloped.

The scarabs vary considerably in habits. Many are dung feeders or feed on decomposing plant materials, carrion, and the like. Some live in the nests or burrows of vertebrates or in the nests of ants or termites. A few feed on fungi. Many feed on plant materials such as grasses, foliage, fruits, and flowers, and some of these are serious pests of lawns, golf greens, or various agricultural crops. The larvae are strongly curved and C-shaped and in many species are the damaging ("white grub") stage.

Key to the Subfamilies of the Scarabaeidae

1.	Pygidium completely covered (or nearly so) by elytra; mostly smaller species (1.5–13 mm long)	**Aphodiinae**	**p. 414**
1′.	Pygidium completely exposed; mostly larger species (longer than 5.0 mm)	2	
2(1′).	Antennal insertion visible from above; clypeus with sides constricted medially just before eyes	**Cetoniinae**	**p. 415**
2′.	Antennal insertion not visible from above; clypeus with sides not constricted	3	
3(2′).	Abdominal sternites distinctly narrowed medially; length of all sternites shorter than length of metasternum; scutellum usually hidden	**Scarabaeinae**	**p. 413**
3′.	Abdominal sternites not narrowed medially; length of all sternites longer than length of metasternum	4	
4(3′).	Claws of both middle and hind tarsi unequal in length and independently movable; tarsomere 5 apically with ventral, median, longitudinal cleft	**Rutelinae**	**p. 414**
4′.	Claws of both middle and hind tarsi equal in length and not independently movable; tarsomere 5 at apex lacking ventral, median, longitudinal cleft, instead with 2 parallel clefts on either side of middle on ventral side	5	
5(4′).	Claws of middle and hind tarsi simple; base of pronotum and elytra subequal in width; apex of hind tibia always with 2 spurs; mandibles often exposed in dorsal view	**Dynastinae**	**p. 415**
5′.	Claws of middle and hind tarsi cleft; apex of hind tibia with 1 or 2 spurs or spurs absent; mandibles not visible in dorsal view	**Melolonthinae**	**p. 414**

Subfamily Scarabaeinae (=Coprinae)—Dung Beetles and Tumblebugs: These beetles are robust, 5–30 mm long, and feed chiefly on dung. Most are dull black, but some are metallic green. The tumblebugs (principally *Canthon* and *Deltochilum*) are black and about 25 mm long or less, with the middle and hind tibiae rather slender, and there are no horns on the head or pronotum. Other genera in this subfamily have the middle and hind tibiae swollen at the tip and often have a horn on the head. In *Phanaeus* (Figure 26–29C,D), which is usually a little less than 25 mm long, the body is a brilliant green with the pronotum golden, and the males have a long horn on the top of the head. The dung beetles in the genera *Copris* and *Dichotomius* (= *Pinotus*) are black, with conspicuous striae on the elytra. *Copris*, about 18 mm long or less, has eight striae on each elytron, and *Dichotomius* (about 25 mm long and very robust) has seven. Other genera in this subfamily are generally shorter than 10 mm.

The tumblebugs are usually common in pastures and are interesting to watch. They chew off a piece of dung, work it into a ball, and roll this ball a considerable distance. They usually work in pairs, one pushing and the other pulling, rolling the ball with their hind legs. The ball is then buried in the soil, and the eggs are laid in the ball. The larvae are thus assured a food supply, and the burial of the ball provides protection.

The sacred scarab of ancient Egypt, *Scarabaeus sacer* L., is a member of this group and has habits similar to those of the tumblebugs. In Egyptian mythology, the ball of dung represented the Sun and its movement across the sky.

Subfamily Aphodiinae—Aphodian Dung Beetles: This is a fairly large group (over 200 North American species) of small dung beetles, and some are quite common, particularly in cow dung. They are usually black, or red and black. One species, *Ataenius spretulus* (Haldeman), has recently become an important pest of turf grasses, especially on golf courses.

Subfamily Melolonthinae—June Beetles, Chafers, and Others: This is a large and widely distributed group, and all its members are plant feeders. Many species are of considerable economic importance. The best-known beetles in this group are the june beetles or may beetles, sometimes called "junebugs," which are usually brown and are common around lights in the spring and early summer (Figure 26–30A). Most belong to the genus *Phyllophaga* (= *Lachnosterna*), which contains more than 200 eastern species. The adults feed at night on foliage and flowers. The larvae (Figure 26–31) are the well-known white grubs that feed in the soil on the roots of grasses and other plants. White grubs are very destructive insects and do a great deal of damage to pastures, lawns, and such crops as corn, small grains, potatoes, and strawberries. The life cycle usually requires two or three years to complete. The greatest damage to field crops occurs when fields are rotated from grass or meadow to corn, another grass.

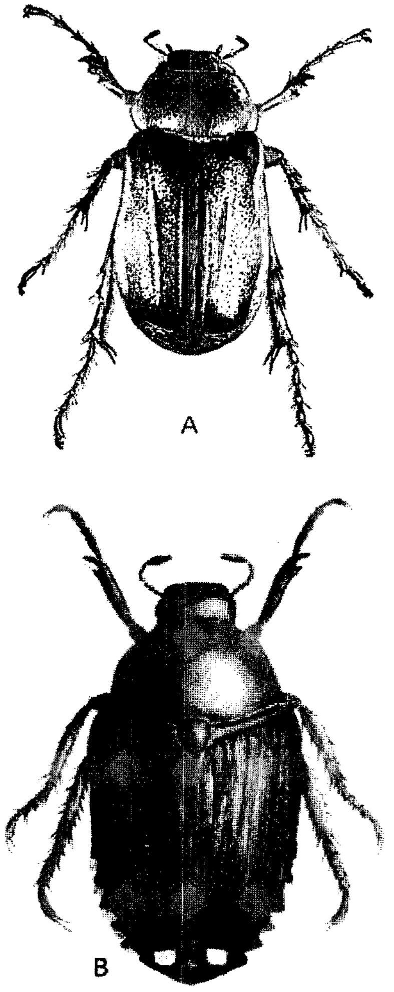

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Figure 26–30 Plant-feeding scarabs. A, a june beetle, *Phyllophaga portoricensis* Smythe (Melolonthinae), $1\frac{1}{2}\times$; B, Japanese beetle, *Popillia japonica* Newman (Rutelinae), $4\frac{1}{2}\times$.

This subfamily also contains the chafers (*Macrodactylus*). The rose chafer, *M. subspinosus* (Fabricius), is a slender, tan, long-legged beetle that feeds on the flowers and foliage of roses, grapes, and various other plants. It often feeds on peaches and other fruits. The larvae are small, white grubs that live in light soil and often seriously damage roots. Poultry that eat these beetles become extremely ill and quite often die.

Most other beetles in this subfamily are robust, oval, and brownish and resemble june beetles (though most are smaller). The beetles in the genus *Dichelonyx* are elongate and slender, with greenish or bronze elytra and simple pretarsal claws.

Subfamily Rutelinae—Shining Leaf Chafers: The larvae of these beetles feed on plant roots, and the adults feed on foliage and fruits. Many adults are very brightly colored. A number of important pest species are included in this subfamily.

One of the most serious pests in this group is the Japanese beetle, *Popillia japonica* Newman (Figure 26–30B). This species was introduced into the eastern United States on nursery stock from Japan in about 1916. Since then, it has spread over a large part of the eastern United States, where it is a serious pest on lawns, golf courses, fruits, and shrubbery. The adult

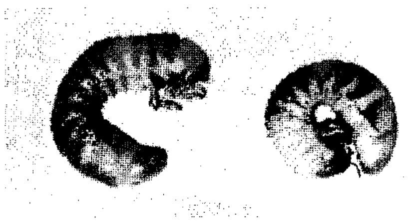

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Figure 26–31 White grubs (*Phyllophaga* sp., Melolonthinae).

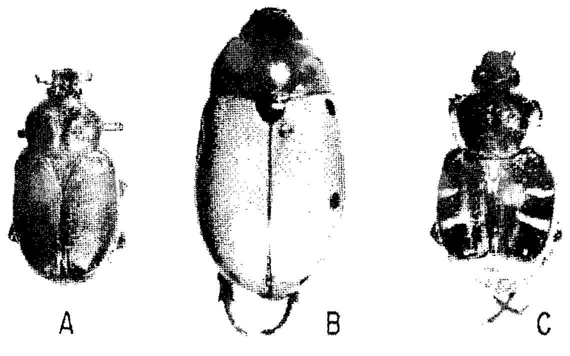

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Figure 26–32 Plant-feeding scarabs. A, the hermit flower beetle, *Osmoderma eremicola* Knoch (Cetoniinae), slightly enlarged; B, the grape pelidnota, *Pelidnota punctata* (L.) (Rutelinae), 1½×; C, a flower beetle, *Trichiotinus texanus* (Horn) (Cetoniinae), 4×.

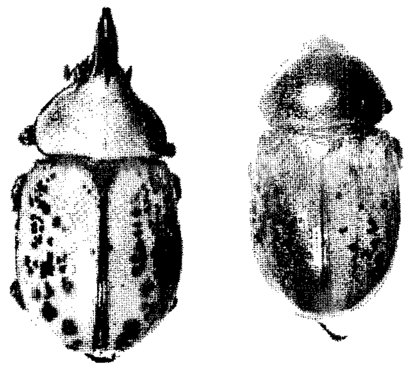

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Figure 26–33 The eastern hercules beetle, *Dynastes tityus* (L.); male at left, female at right. About natural size.

is very pretty. The head and thorax are bright green, the elytra are brownish tinged with green on the edges, and there are white spots along the sides of the abdomen. This species has one generation a year and overwinters in the larval stage in the soil.

Another rather common and destructive species is the grape pelidnota, *Pelidnota punctata* (L). The adult is 25 mm or more in length and looks a little like a large june beetle, but is yellowish with three black spots on each elytron (Figure 26–32B). Most damage done by this species is done by the adult. The larvae feed chiefly in rotting wood.

The members of the genus *Cotalpa* are usually large beetles, uniform green or yellowish above and dark beneath. The larvae do considerable damage to the roots of berries, corn, and grass. One distinctive species in this genus is *C. lanigera* (L.), 20–26 mm long and entirely yellow with a metallic luster. It lives on or near catalpa trees.

From Baja California to Utah, the common members of the Rutelinae are the black and reddish brown members of the genus *Paracotalpa*. In Texas and Arizona are found the real jewels of this subfamily, species belonging to the genus *Chrysina* (= *Plusiotis*). These large scarabs are a brilliant green, sometimes with added longitudinal lines of metallic golden color. They are favored items among collectors.

Subfamily Dynastinae—Rhinoceros Beetles, Hercules Beetles and Elephant Beetles: This group contains some of the largest North American beetles, a few of which may reach a length of 65 mm. The dorsal surface of the body is rounded and convex, and the males usually have horns on the head or pronotum (Figure 26–33). The females lack these horns.

The largest Dynastinae are the Hercules beetles (*Dynastes*), which occur principally in the southern states. *Dynastes tityus* (L.), the eastern species, is 50–65 mm long and greenish gray mottled with large black areas. The pronotal horn of the male extends forward over the head (Figure 26–33). The western species, *D. granti* Horn, is similar, but is slightly larger and has a longer pronotal horn. The elephant beetles (*Strategus*) are big brown scarabs, 35–50 mm long, that occur from Rhode Island to Kansas and Texas. They have three horns on the pronotum in the male (one in the female), but none on the head. In the rhinoceros beetle, *Xyloryctes jamaicensis* (Drury), a dark brown scarab a little over 25 mm long, the males have a single large, upright horn on the head. The females have a small tubercle instead of a horn. The larva of this species feeds on the roots of ash trees. The rhinoceros beetle occurs from Connecticut to Arizona. The members of the genus *Phileurus*, which are about 25 mm long and have two horns on the head, occur in the South and Southwest.

The smaller members of this subfamily, particularly the species in the genera *Ligyrus* and *Euetheola*, are often serious pests of corn, sugarcane, and cereal crops. Both adult and larval stages cause damage.

Subfamily Cetoniinae—Flower Beetles and Others: The members of this group are principally pollen feeders and are common on flowers. Many live under loose bark or in debris, and a few live in ant nests. The larvae feed on organic matter in the soil, and some species damage the roots of plants. This subfamily includes the goliath beetles of Africa, which are among the largest insects known. Some species reach a length of 100 mm or more.

Several genera in this subfamily (including *Cotinis*, *Euphoria*, and *Cremastocheilus*) have the mesepimera visible from above, between the hind angles of the

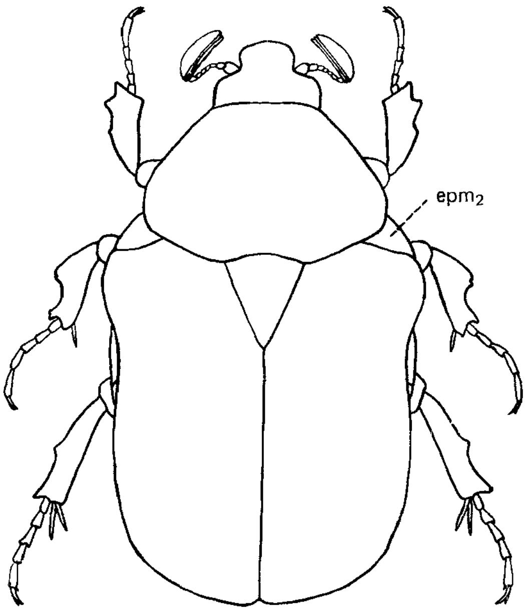

Figure 26–34 A bumble flower beetle, *Euphoria inda* (L.) (Cetoniinae), 5×. *epm*$_2$, mesepimeron.

pronotum and the humeri of the elytra (Figure 26–34). The members of the genus *Cotinis* are more than 18 mm long, and the small scutellum is covered by a median backward-projecting lobe of the pronotum. Those of *Euphoria* and *Cremastocheilus* are smaller and have a large, exposed scutellum (Figure 26–34). The green june beetle, *Cotinis nitida* (L.), is a common dark-green beetle nearly 25 mm long. The adults feed on grapes, ripening fruits, and young corn, and the larvae often seriously damage lawn, golf courses, and various crops.

The beetles in the genus *Euphoria* are somewhat bumblebee-like and are often called "bumble flower beetles." They are brownish yellow and black, are very pubescent, and act much like bumblebees. These beetles do not extend their elytra in flight. Instead, the hind wings are extended through shallow emarginations at the sides of the elytra (Figure 26–34).

Perhaps the least-known and most interesting members of this subfamily are those in the genus *Cremastocheilus*. These beetles, which are 9–15 mm long, are kept captive in ant nests to provide the ants with a nutritive fluid. The ants cling to the beetle's thorax and gnaw at pubescent glandular areas on the exposed mesepimera. More than 30 species belonging to this genus are known in the United States.

In the other common genera of Cetoniinae, the mesepimera are not visible from above. The hermit flower beetle, *Osmoderma eremicola* Knoch, is a brownish black insect about 25 mm long, with the elytra longer than wide (Figure 26–32A). The larvae feed in decaying wood, and the adults are frequently found under dead bark or in tree cavities. The adults emit a very disagreeable odor when disturbed. In *Valgus* and *Trichiotinus*, the elytra are about as long as wide. The members of *Valgus* are small, less than 7.5 mm long, and are brown and covered with scales. *Trichiotinus* beetles are brightly colored and pubescent (Figure 26–32C). The adults of these two genera live on various types of flowers, and the larvae live in decaying wood.

Family **Eucinetidae—Plate-Thigh Beetles:** The eucinetids are small (2.5–3.0 mm long), oval, convex beetles that have the head deflexed and not visible from above (Figure 26–35A). There are six visible abdominal sterna, and the hind coxae are dilated into broad plates that extend to the elytra and cover most of the first visible abdominal sternum (hence the common

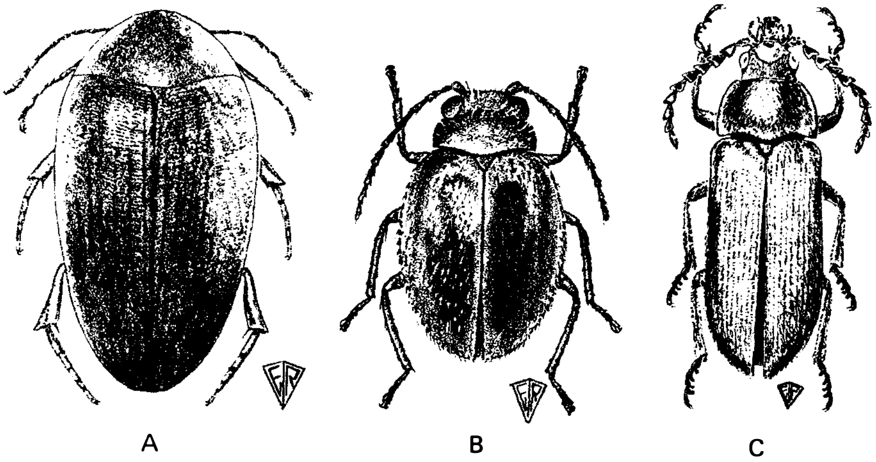

Figure 26–35 A, a plate-thigh beetle, *Eucinetus terminalis* LeConte (Eucinetidae), 16×; B, a marsh beetle, *Prionocyphon limbatus* LeConte (Scirtidae), 6×; C, a soft-bodied plant beetle, *Dascillus davidsoni* LeConte (Dascillidae), 3×. (Courtesy of Arnett.)

name). Eleven species occur in North America, and they are generally found under bark or in fungi.

Family **Clambidae—Minute Beetles:** The clambids are minute (about 1 mm long), oval, convex, brownish to black beetles that are capable of tucking the head and prothorax under the body and rolling into a ball. They resemble the leiodids in this respect, but differ from leiodids in being pubescent, in having the hind coxae dilated into broad plates, and in having a fringe of long hairs on the hind wings. These beetles live in decaying plant material. The group is small (12 North American species), and its members are not often encountered.

Family **Scirtidae—Marsh Beetles:** The scirtids are oval beetles, 2–4 mm long (Figure 26–35B), and live on vegetation in swampy places and in damp, rotting debris. There are 50 species in North America. Some have enlarged hind femora and are active jumpers. The larvae, which have long, slender antennae, are aquatic.

Family **Dascillidae—Soft-Bodied Plant Beetles:** The dascillids are oval to elongate, soft-bodied, pubescent beetles, mostly 3–14 mm long. The head is usually visible from above, and some species have relatively large and conspicuous mandibles (Figure 26–35C). They are most likely to be found on vegetation near water, but are not very common. This group contains five North American species in Arizona and California.

Family **Rhipiceridae—Cicada Parasite Beetles:** These are elongate-oval, brownish beetles, 12–24 mm long, with orange antennae and prominent mandibles (Figure 26–36). The antennae are flabellate in the male and serrate to pectinate in the female. These beetles superficially resemble june beetles and are good fliers. The larvae are parasites of cicada nymphs. This group is small (five North American species of *Sandalus*) but is widely distributed.

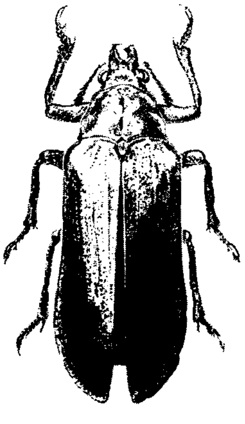

Figure 26–36 A cicada parasite beetle, *Sandalus petrophya* Knoch, female (Rhipiceridae), 3×. (Courtesy of Arnett.)

Family **Buprestidae—Metallic Wood-Boring Beetles:** The adults of this group are 3–100 mm (usually less than 20 mm) in length and are often rather metallic—coppery, green, blue, or black—especially on the ventral side of the body and on the dorsal surface of the abdomen. They are hard-bodied and compactly built and usually have a characteristic shape (Figures 26–37 and 26–38). Many adult buprestids are attracted to dead or dying trees and logs and to slash. Others live on the foliage of trees and shrubs. These beetles run or fly rapidly and are often difficult to catch. Some are colored like the bark and are very inconspicuous when they remain motionless. Many of the larger beetles in this group are common in sunny situations. There are about 762 North American species of Buprestidae.

Most buprestid larvae bore under bark or in wood, attacking either living trees or newly cut or dying logs and branches. Many do serious damage to trees and shrubs. The eggs are usually laid in crevices in the bark. The larvae, on hatching, tunnel under the bark, and some species eventually bore into the wood. The galleries under the bark are often winding and filled with frass. The galleries in the wood are oval in cross section and usually enter the wood at an angle (Figure 26–39). Pupation occurs in the galleries. Because buprestid larvae usually have the anterior end expanded and flattened (Figure 26–40), they are often known as "flat-headed borers." The larvae of some species make winding galleries under the bark of twigs (Figure 26–41B); others make galls (Figure 26–41A); and one species girdles twigs.

The larvae of *Chrysobothris femorata* (Olivier) attack a number of trees and shrubs and frequently do serious damage to fruit trees. The larvae of different species of *Agrilus* attack raspberries, blackberries, and other shrubs. *Agrilus champlaini* Frost makes galls in ironwood (Figure 26–41A), and *A. ruficollis* (Fabricius) makes galls in raspberry and blackberry. *Agrilus arcuatus* (Say) is a twig girdler. The adults of the genus *Agrilus* are rather long and narrow (Figure 26–38C); most are dark-colored with metallic shades, and some have light markings. The emerald ash borer, *Agrilus planipennis* Fairmaire, an iridescent green species, was recently introduced into the Midwest (Michigan and Ohio at this time) and threatens to become a major pest of ash. The larvae of the species of *Brachys* (Figure 26–37D) are leaf miners. Most buprestids fly when disturbed, but the beetles in the genus *Brachys* draw up their legs, "play dead," and fall off the foliage onto the ground. These smaller buprestids are usually found on foliage.

Family **Byrrhidae—Pill Beetles:** The pill beetles (Figure 26–42) are oval, convex, and 1.5 to 10.0 mm long. The head is bent downward and concealed from above, and the wide hind coxae extend to the elytra. These in-

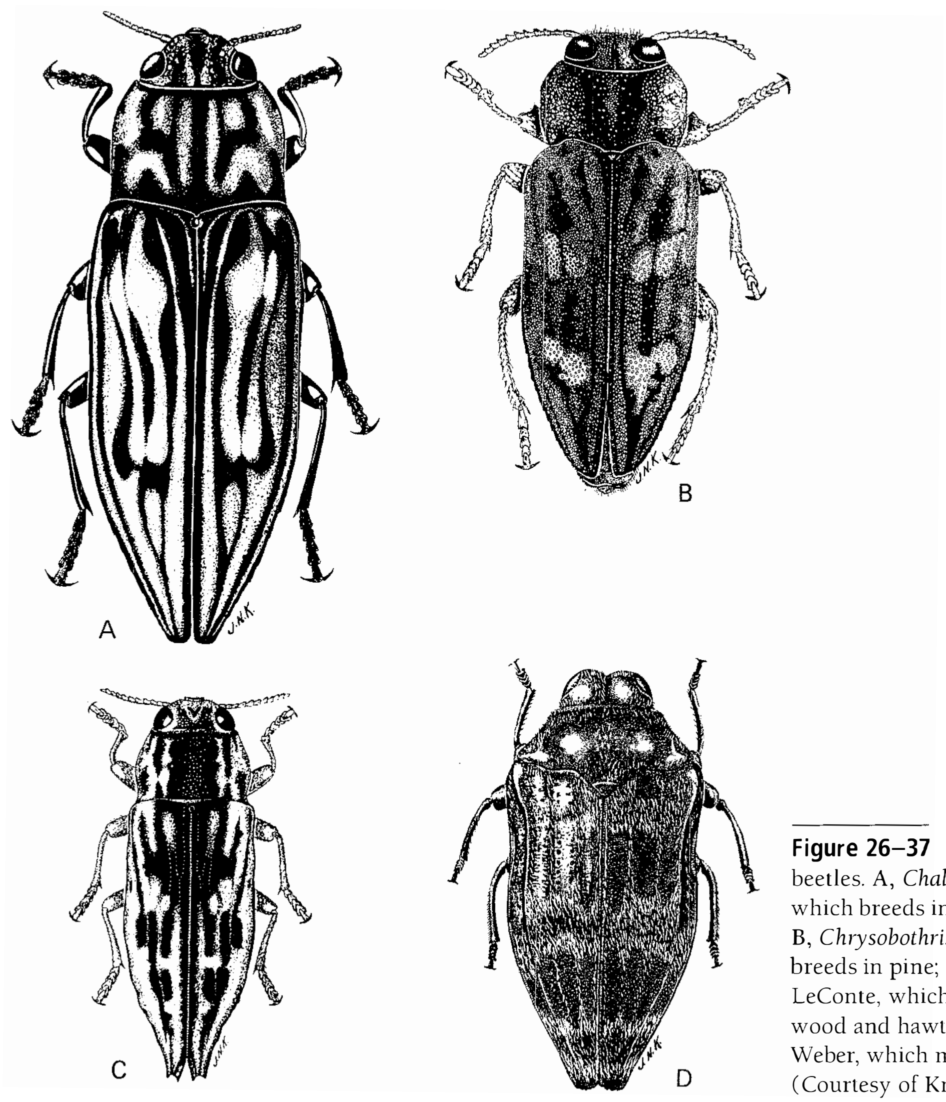

Figure 26–37 Metallic wood-boring beetles. A, *Chalcophora fortis* LeConte, which breeds in dead white pine; B, *Chrysobothris floricola* Gory, which breeds in pine; C, *Dicerca lepida* LeConte, which breeds in dead ironwood and hawthorn; D, *Brachys ovatus* Weber, which mines in oak leaves. (Courtesy of Knull.)

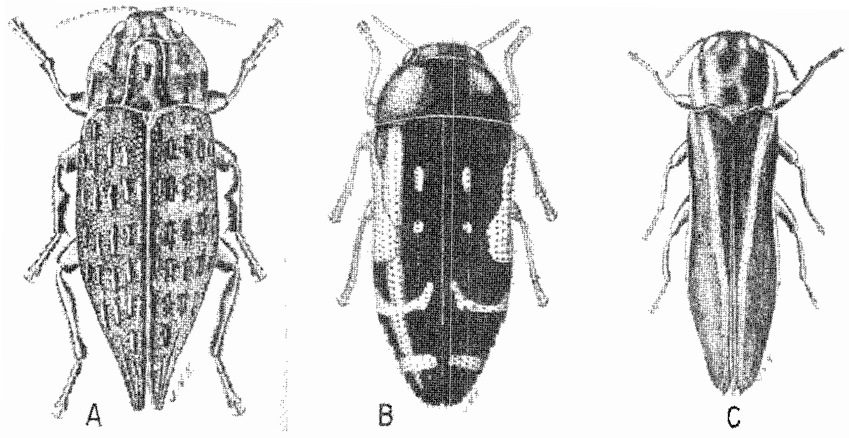

Figure 26–38 Metallic wood-boring beetles. A, *Dicerca tenebrosa* (Kirby), 3½×; B, *Acmaeodera pulchella* (Herbst), 6×; C, *Agrilus bilineatus* (Weber), 6×. (Courtesy of Knull.)

sects usually live in sandy situations, such as lake shores, where they can be found under debris. Species of *Byrrhus* and *Cytilus* occasionally damage forest tree seedlings. When disturbed, they draw in their legs, with the femora fitting into coxal grooves, and remain motionless. There are 35 species recorded for the United States and Canada.

***Family* Elmidae—Riffle Beetles:** These beetles generally live on the stones or debris in the riffles of streams. A few species live in ponds or swamps, and a few are terrestrial. Riffle beetles are somewhat cylindrical in shape, with a very smooth or somewhat ridged elytra (Figure 26–43C), and most are 3.5 mm long or less. The larvae of most species, which live in the same situations as the adults, are long and slender. Those of *Phanocerus* are somewhat flattened and elliptical. There are 85 species in the United States and Canada.

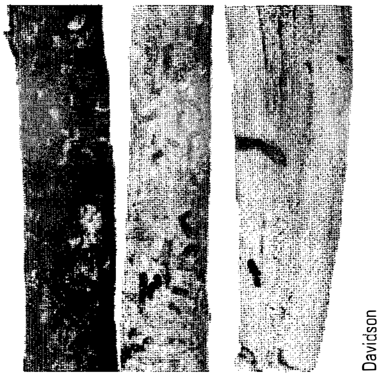

Figure 26–39 Galleries of buprestid larvae.

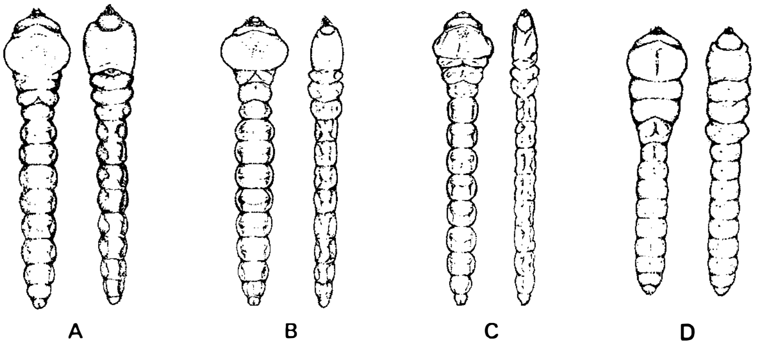

Figure 26–40 Larvae of Buprestidae. A, *Chrysobothris trinerva* (Kirby); B, *Melanophila drummondi* (Kirby); C, *Dicerca tenebrosa* (Kirby); D, *Acmaeodera prorsa* Fall. Dorsal view at left in each figure, lateral view at right. (Courtesy of USDA.)

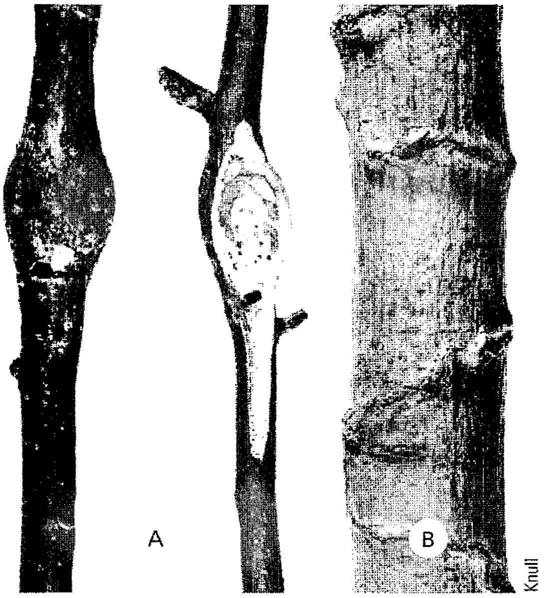

Figure 26–41 A, galls of *Agrilus champlaini* Frost, in ironwood (*Ostrya*); B, the work of *Agrilus bilineatus carpini* Knull on blue beech (*Carpinus*).

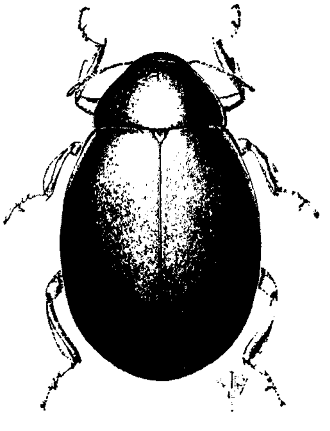

Figure 26–42 A pill beetle, *Amphicyrta dentipes* Erichson, 5×. (Courtesy of Arnett.)

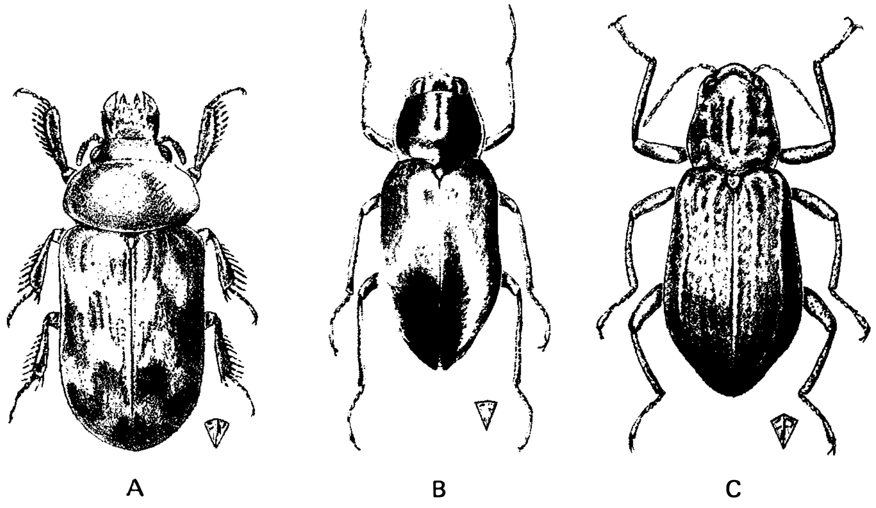

Figure 26–43 A, a variegated mud-loving beetle, *Neoheterocerus pallidus* (Say) (Heteroceridae), 9×; B, a long-toed water beetle, *Helichus lithophilus* (Germar) (Dryopidae), 8×; C, a riffle beetle, *Stenelmis crenata* (Say) (Elmidae), 8×. (Courtesy of Arnett.)

***Family* Dryopidae—Long-Toed Water Beetles:** The dryopids are elongate-oval, 1–8 mm long, and dull gray or brown, with the head more or less withdrawn into the prothorax (Figure 26–43B). The body in some species is covered with a fine pubescence. The antennae are very short, with most antennomeres broader than long, and are concealed beneath the prosternal lobe. These beetles usually cling to objects in a stream. Sometimes they are found crawling around on the bottoms of streams or along the shores. The adults may leave the stream and fly about, especially at night. Most known larvae are vermiform and live in soil or decaying wood (rather than in water). Thirteen species occur in North America.

***Family* Lutrochidae—Travertine Beetle:** The small size (2–6 mm long), dense pubescence, stout body, very short antennae, and elongate mandibles characterize members of this small family, which contains three species of *Lutrochus* in North America. Both adults and larvae are aquatic and feed on algae and waterlogged wood.

***Family* Limnichidae—Minute Marsh-Loving Beetles:** The members of this and the two following families have quite long pretarsal claws (as in Figure 26–10H), and the first three visible abdominal sterna are more or less fused together. The larvae of most species (and usually also the adults) are aquatic. The limnichids are small (1–4 mm long), oval, convex beetles whose body is clothed with fine pubescence. The most common limnichids (*Lutrochus*) have 11 antennomeres. These beetles are usually found in the wet sand or soil along the margins of streams. There are 28 species in the United States.

***Family* Heteroceridae—Variegated Mud-Loving Beetles:** The heterocerids are a group of flattened, oblong, pubescent beetles (Figure 26–43A) that live in mud or sand along the banks of streams or lakes. Superficially they resemble small scarabs. Most are blackish or brownish, with bands or spots of dull yellow, and are 4–6 mm long. The tibiae are armed with rows of heavy, flattened spines. The tarsi are 4-4-4, with tarsomeres 1 and 4 much longer than 2 and 3. The antennae are short, with the last seven antennomeres forming an oblong serrate club. The front and middle tibiae are greatly dilated and spiny, and are used in burrowing. When the shore is flooded with water splashed up from the stream, these beetles may often be forced to leave their burrows in the stream bank. There are 34 species in the United States and Canada.

***Family* Psephenidae—Water-Penny Beetles:** These beetles derive their common name from the peculiar shape of the larvae (Figure 26–44A,B). The larvae (called "water pennies") are very flat and almost circular and live on the undersides of stones or other objects in streams and wave-swept shores. *Psephenus herricki* (DeKay) is a common eastern species. The adult is a somewhat flattened, blackish beetle, 4–6 mm long (Figure 26–44C), which is usually found on stones in the water or along the shore of the streams where the larvae live. Fifteen other species, mostly western, occur in the United States.

***Family* Ptilodactylidae:** The members of this group are elongate-oval in shape, brownish, 4–6 mm long, and the head is generally not visible from above. The antennae are serrate in the female and pectinate in the male (antennomeres 4–10 each bear a slender basal process about as long as the antennomere). The tarsi are 5-5-5, with the third tarsomere lobed beneath and the fourth often minute. The ptilodactylids live on vegetation, chiefly in swampy places. Some larvae are

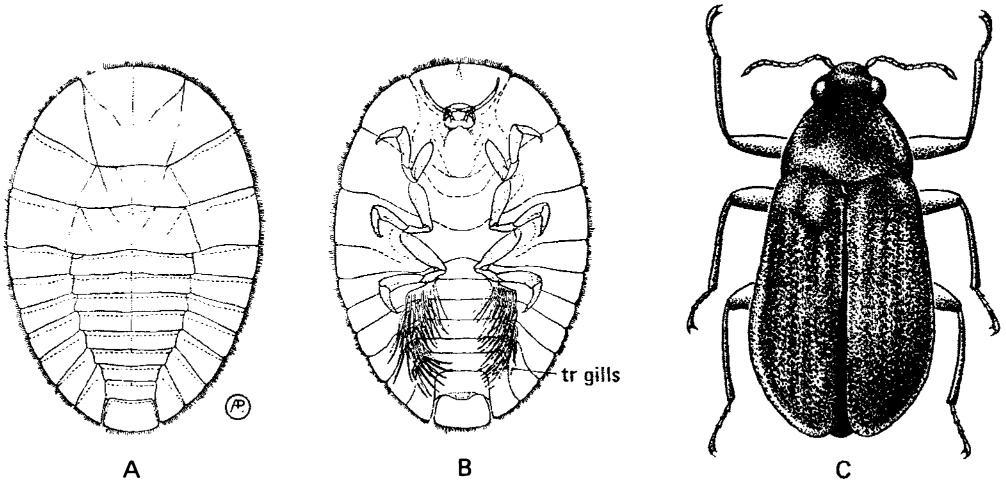

Figure 26–44 Psephenidae. A, dorsal view, and B, ventral view, of a water penny, the larva of *Psephenus herricki* (DeKay); C, adult water penny beetle, *Psephenus herricki* (DeKay), 8×. *tr gills*, tracheal gills. (A and B, courtesy of Peterson; C, courtesy of Arnett.)

aquatic, and others live in moist, dead logs. There are 28 species in six genera in North America.

***Family* Chelonariidae—Turtle Beetles:** Only one rare species of chelonariid occurs in the United States, *Chelonarium lecontei* Thomson, which occurs in the Southeast, from North Carolina to eastern Texas and south to Florida and Louisiana. This insect is oval, convex, 4–5 mm long, and black with patches of white pubescence on the elytra. The legs are retractile. The head is retracted into the prosternum, exposing only the eyes and antennae. The basal antennomeres are situated in a prosternal groove, and the remaining antennomeres extend back along the mesosternum. The larvae of these beetles are aquatic, and the adults are found on vegetation.

***Family* Eulichadidae:** This group includes a single North American species, *Stenocolus scutellaris* LeConte, which has previously been included in the family Dascillidae. This species, which occurs in the mountains of northern California, is 15–26 mm long and shaped like a click beetle, with a vestiture of fine hairs. The mandibles are prominent and strongly bent apically, with the apex scooplike. The larvae, which are the overwintering stage, live in streams and probably feed on decaying vegetation.

***Family* Callirhipidae:** The only North American species in this family is *Zenoa picea* (Beauvois), an elongate, dark-brown, shiny beetle, 11–15 mm long. Its antennae are serrate (males) to pectinate (females). This is a rare beetle found under logs and bark and is known from Ohio, Indiana, Pennsylvania, Kansas, Louisiana, and Florida.

***Family* Artematopodidae:** This is a small family (eight North American species) formerly placed in the Dascillidae (subfamily Dascillinae), which they strongly resemble. They are elongate, pubescent beetles, 4.0 to 7.5 mm long, with the head deflexed and with long, filiform antennae. The tarsi usually have a small fourth tarsomere, and tarsomeres 2 to 4 are lobed. Collectors frequently take individuals of *Eurypogon* species by sweeping vegetation.

***Family* Brachypsectridae—The Texas Beetle:** This family is represented in the United States by a single, very rare species, *Brachypsectra fulva* LeConte, a yellowish brown beetle 5–6 mm long, which is sometimes called the Texas beetle. It resembles a click beetle in general appearance, but does not have the prosternal spine and mesosternal fossa characteristic of the Elateridae. This insect is known from Texas, Utah, Colorado, New Mexico, and California.

***Family* Cerophytidae:** This group includes two very rare species of *Cerophytum*, one occurring in the East and the other in California and Oregon. These beetles are elongate-oblong in shape, somewhat flattened, 7.5 to 8.5 mm long, and brownish to black. The hind trochanters are very long, nearly as long as the femora. Adults can "jump" in the same manner as click beetles. These beetles live in rotten wood and under dead bark.

***Family* Eucnemidae—False Click Beetles:** This family (85 species in North America) is very closely related to the Elateridae. Its members are relatively rare beetles usually found in wood that has just begun to decay, chiefly in beech and maple. Most are brownish and

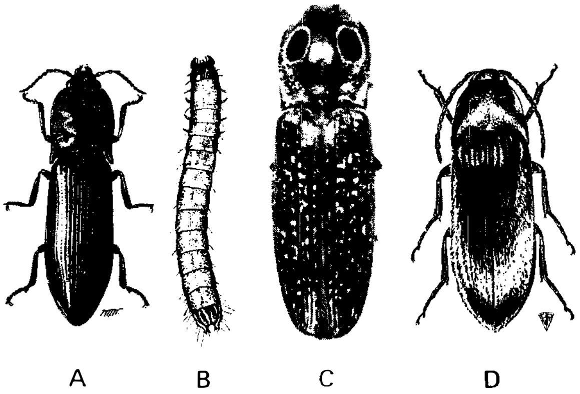

Figure 26–45 A, adult, and B, larva, of a click beetle, *Ctenicera noxia* (Hyslop) (slightly enlarged); C, the eyed click beetle, *Alaus oculatus* (L.) (about natural size); D, a false click beetle, *Anelastes druryi* (Kirby), 3×. (A and B, courtesy of USDA; D, courtesy of Arnett.)

about 10 mm long or less (Figure 26–45D). The pronotum is quite convex above; the antennae are inserted rather close together on the front of the head; and there is no distinct labrum. The pretarsal claws are serrate in the genus *Perothops*, previously placed in a separate family. These beetles quiver their antennae almost constantly, unlike the Elateridae. Some, like the click beetles, can click and jump.

***Family* Throscidae:** This is a small group (20 North American species) of oblong-oval brownish to black beetles that are mostly 5 mm long or less. They are similar to the elaterids, but more oval. Some (*Aulonothroscus* and *Trixagus*) have clubbed antennae. The prosternum is lobed anteriorly and almost conceals the mouthparts. The prothorax appears rather solidly fused to the mesothorax, but at least some of these beetles can click and jump like elaterids. The adults are found chiefly on vegetation and in leaf litter. They are primarily in litter in cool weather, but fly or climb onto nearby vegetation in warm weather. They do not seem to have any preferences for particular species of plants.

***Family* Elateridae—Click Beetles:** The click beetles constitute a large group (about 965 Nearctic species), and many species are quite common. These beetles are peculiar in being able to "click" and jump. In most related groups, the union of the prothorax and mesothorax is such that little or no movement at this point is possible. The clicking is made possible by the flexible union of the prothorax and mesothorax, and by a prosternal spine that fits into a groove on the mesosternum (Figure 26–8A).

If one of these beetles is placed on its back on a smooth surface, it is usually unable to right itself by means of its legs. It bends its head and prothorax backward, so that only the extremities of the body are touching the surface on which it rests. Then, with a sudden jerk and clicking sound, it straightens out its body. This movement snaps the prosternal spine into the mesosternal groove and throws the insect into the air, spinning end over end. If the insect does not land right side up, it continues snapping until it does.

The click beetles can usually be recognized by their characteristic shape (Figure 26–45A,C). The body is elongate, usually parallel-sided, and rounded at each end. The posterior corners of the pronotum are prolonged backward into sharp points or spines. The antennae are usually serrate (occasionally filiform or pectinate). Most of these beetles are between 12 and 30 mm long, but a few exceed these limits. The largest and most easily recognized species is the eyed click beetle, *Alaus oculatus* (L.), a mottled-gray beetle with the pronotum bearing two large, black, eyelike spots (Figure 26–45C). This species may reach about 40 mm or more in length. Most elaterids are inconspicuously colored with black or brown.

Adult click beetles are phytophagous and live on flowers, under bark, or on vegetation. Most larvae are slender, hard-bodied, and shiny and are commonly called "wireworms" (Figure 26–45B). The larvae of many species are very destructive, feeding on newly planted seeds and the roots of beans, cotton, potatoes, corn, and cereals. Many elaterid larvae live in rotting logs, and some of these feed on other insects. Pupation occurs in the ground, under bark, or in dead wood.

Species of *Pyrophorus* in the southern states and in the tropics have two light-producing spots on the posterior edge of the prothorax and one on the abdomen. The light is much stronger than that of the lampyrids, and a large number flying about at night is a striking sight.

Members of the subfamily Cebrioninae are elongate, brownish beetles, 15–25 mm long, with hooklike mandibles extending forward in front of the head. Some have a quite hairy body. The larvae and females (which are wingless) live in the ground. The males are excellent fliers and are largely nocturnal. All 30 North American species are southern or southwestern.

***Family* Lycidae—Net-Winged Beetles:** The lycids (76 North American species) are elongate soft-winged beetles, 5–18 mm long. They are somewhat similar to the soldier beetles, but may be readily recognized by the peculiar network of raised lines on the elytra, with the longitudinal ridges more distinct than the transverse ridges (Figure 26–46A). Some western species (*Lycus*) have a distinct snout. The elytra in some species are slightly widened posteriorly. The adults live on foliage and tree trunks, usually in wooded areas. They feed on the juices of decaying plant materials and occasionally on other insects. The larvae are predaceous. One of the more common members of this

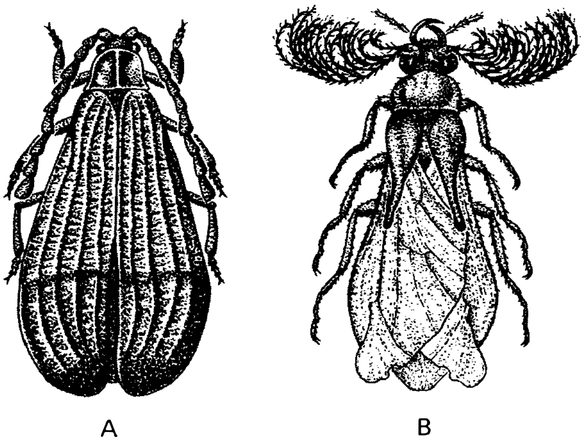

Figure 26–46 A, a net-winged beetle, *Calopteron terminale* (Say); B, adult male of a glow-worm, *Phengodes plumosa* Olivier; 4×. (Courtesy of Arnett.)

group is *Calopteron reticulatum* (Fabricius), 11–19 mm long. The elytra are yellow, with the posterior half and a narrow cross band in the anterior part black. This insect's pronotum is black, with a yellow margin. Most lycids are blackish, but many are brightly colored with red, black, or yellow. They are apparently distasteful to predators, and their coloration is mimicked by other beetles (certain Cerambycidae) and some moths (for example, certain Arctiidae; Figure 30–82C).

***Family* Telegeusidae:** The Telegeusidae are represented in North America by two species of small, rare beetles that occur in Arizona and California. Their most distinctive character is the form of the maxillary and labial palps, which have the terminal segment tremendously enlarged. The tarsi are five-merous, the antennae are serrate, and the seven or eight abdominal segments are less than half covered by the short elytra. The telegeusids are slender and 5–8 mm long, resembling small rove beetles. The hind wings do not fold, but extend back over the abdomen beyond the tips of the elytra. Females, which are probably larviform, and larvae of telegeusids are unknown.

***Family* Phengodidae—Glowworms:** This is a small group (23 species in North America) of relatively uncommon beetles closely related to the Lampyridae. Most are broad and flat, with the elytra short and pointed and the posterior part of the abdomen covered only by the membranous, fan-shaped, nonfolding hind wings (Figure 26–46B). The antennae are usually serrate, but in some males they may be pectinate or plumose. These insects vary in length from 10 to 30 mm and are found on foliage or on the ground. The adult females of all known species are wingless and luminescent, as in the Lampyridae, and look much like larvae. The larvae are predaceous.

***Family* Lampyridae—Lightningbugs, Fireflies:** Many members of this common and well-known group have "tail light"—segments near the end of the abdomen with which the insects produce light. These luminous segments can be recognized, even when they are not glowing, by their yellowish green color. During certain seasons, usually early summer, these insects fly about in the evenings and are conspicuous by their blinking yellow lights.

The lampyrids are elongate and very soft-bodied beetles, 5–20 mm long, in which the pronotum extends forward over the head so that the head is largely or entirely concealed from above (Figure 26–47A). The elytra are soft, flexible, and rather flat except for the epipleurae. Most larger members of this group have luminescent organs, but many smaller ones do not.

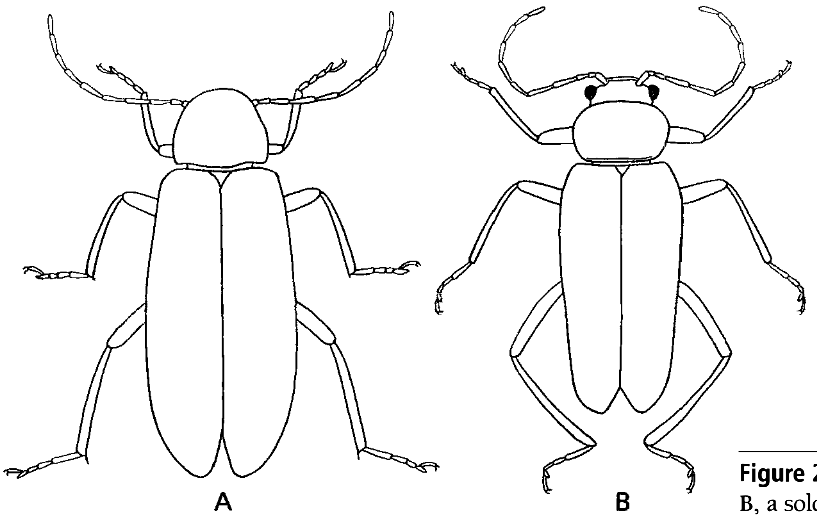

Figure 26–47 A, a lightningbug (*Photuris*); B, a soldier beetle (*Chauliognathus*); 3.75×.

The light emitted by these insects is unique in being cold. Nearly 100% of the energy given off appears as light. In electric lights, only 10% of the energy is light, and the other 90% is given off as heat. Firefly light is produced by the oxidation of a substance called *luciferin,* made in the cells of the light-producing organs. These organs have a rich tracheal supply, and the insect controls light emission by controlling air supply to the organs. When air is admitted, the luciferin (in the presence of an enzyme called *luciferinase* or *luciferase*) is almost instantly oxidized, releasing energy as light. The flashing of fireflies serves primarily as a means of getting the sexes together, and each species has a characteristic flash rhythm. Females of some predatory species imitate the flashes of other species and thus lure amorous but hapless males of those species to their doom.

During the day the lampyrids are usually found on vegetation. The larvae are predaceous and feed on various smaller insects and on snails. The females of many species are wingless and look very much like larvae. These wingless females and most lampyrid larvae are luminescent and are often called "glowworms." There are about 125 species of fireflies in the United States and Canada, mostly in the East and the South.

***Family* Omethidae—False Firefly Beetles, False Soldier Beetles:** The omethids are soft-bodied beetles resembling lampyrids or cantharids, with which they are sometimes associated. There are 10 species in seven genera in the United States. Little is known about their ecology or feeding habits. They have been collected on foliage during the day, and some have been collected from forest floor debris.

***Family* Cantharidae—Soldier Beetles:** The cantharids are elongate, soft-bodied beetles, 1–15 mm long, that are very similar to the lightningbugs (Lampyridae), but the head protrudes forward beyond the pronotum and is visible from above (not concealed by the pronotum as in the Lampyridae). These beetles do not have light-producing organs.

Adult soldier beetles are usually found on flowers. The larvae are predaceous on other insects. One common species, *Chauliognathus pennsylvanicus* (DeGeer) (Figure 26–47B), about 13 mm long, has each elytron yellowish with a black spot or stripe. Members of other genera are yellowish, black, or brown. There are 473 species of soldier beetles in North America.

***Family* Jacobsoniidae—Jacobson's Beetles:** These tiny beetles (less than 1 mm long) may be recognized by the elongate form, lack of a scutellum, a metasternum as long as or longer than all five ventrites combined, and a one- or two-merous antennal club. Their relationships with other beetle families are unclear. Two species of *Derolathrus,* recently reported from southern Florida, were caught in flight intercept traps (Peck and Thomas 1998). At least one seems to have become established.

***Family* Derodontidae—Tooth-Necked Fungus Beetles:** The derodontids (9 North American species) are small, usually brownish beetles, 3–6 mm long (Figure 26–48), and have a pair of ocelli on the head near the inner margins of the compound eyes (Figure 26–13C). The members of the genus *Derodontus* have three or four strong teeth or notches along the lateral margins of the pronotum. Other genera lack these teeth. The elytra completely cover the abdomen, and each bears many rows of large square punctures or polished dark spots. These beetles live in woody fungi and under the bark of rotting logs. *Laricobius erichsonii* Rosenhauer has been introduced from Europe into Oregon, where it is established as an important predator of the balsam woolly aphid.

***Family* Nosodendridae—Wounded Tree Beetles:** This family includes two species of *Nosodendron,* one occurring in the East and the other in the West. The eastern species, *N. unicolor* Say, is an oval, convex, black beetle 5–6 mm long. It lives in oozing tree wounds (sometimes in good numbers), under the bark of dead logs, and in debris. The nosodendrids are similar to the Byrrhidae, but the head is visible from above, and the elytra bear rows of short, yellow hair tufts.

***Family* Dermestidae—Dermestid or Skin Beetles:** This group (123 North American species) contains a number of very destructive and economically important species. The dermestids are mostly scavengers and feed on a great variety of plant and animal products, including leather, furs, skins, museum specimens, woolen or silk materials, rugs, stored food materials, and carrion. Most of the damage is done by the larvae.

Adult dermestids are small, oval, or elongate-oval, convex beetles with short clubbed antennae, and they vary in length from 2 to 12 mm. They are usually hairy

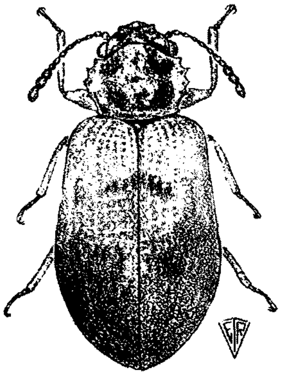

Figure 26–48 A tooth-necked fungus beetle, *Derodontus maculatus* Melsheimer, 15×. (Courtesy of Arnett.)

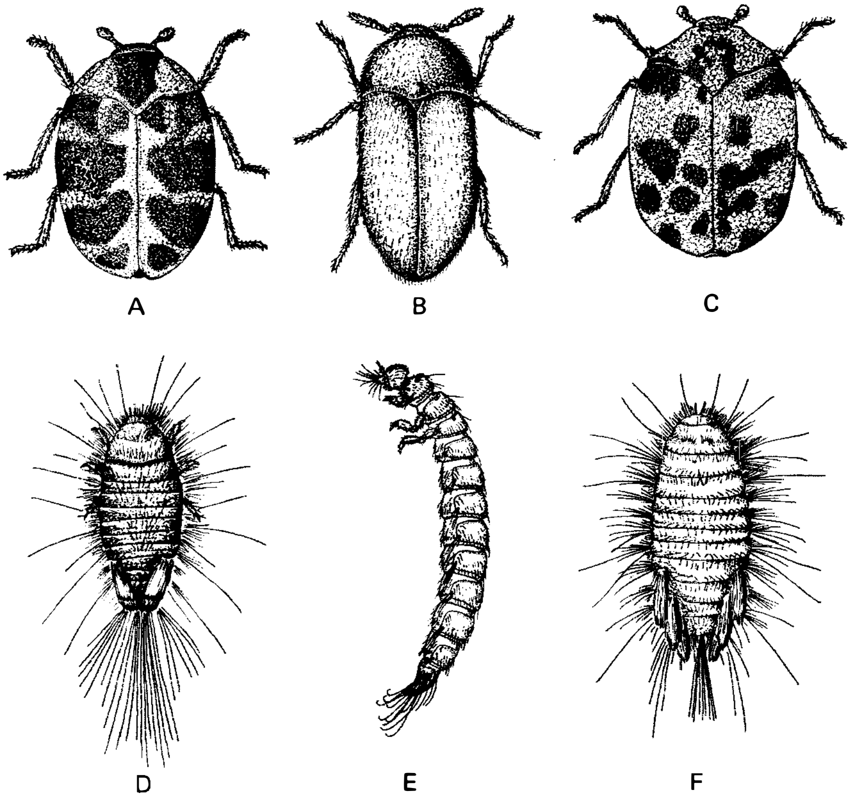

Figure 26–49 Dermestid beetles. A, the carpet beetle, *Anthrenus scrophulariae* (L.), adult; B, the black carpet beetle, *Attagenus megatoma* (Fabricius), adult; C, the furniture carpet beetle, *Anthrenus flavipes* LeConte, adult; D, larva of *A. scrophulariae* (L.), dorsal view; E, larva of *A. megatoma* (Fabricius), lateral view; F, larva of *A. flavipes* LeConte, dorsal view. (E, courtesy of Peterson; other figures, courtesy of the Cornell University Agricultural Experiment Station.)

or covered with scales (Figure 26–49A–C). All adults except members of the genus *Dermestes* have a median ocellus (which is sometimes very small). They may be found in the materials mentioned previously, and many feed on flowers. Some are black or dull-colored, but many have a characteristic color pattern. The larvae are usually brownish and are covered with long hairs (Figure 26–49D–F).

The larger dermestids belong to the genus *Dermestes*. The larder beetle, *D. lardarius* L., is a common species in this genus. It is a little more than 6 mm long and is black with a light brown band across the base of the elytra. It feeds on a variety of stored foods, including meats and cheese, and occasionally damages the specimens in insect collections.

Some of the smaller dermestids are often common in houses and may do serious damage to carpets, upholstery, and clothing. Two common species of this type are the black carpet beetle, *Attagenus megatoma* (Fabricius) and the carpet beetle, *Anthrenus scrophulariae* (L.). The former is a grayish black beetle, 3.5–5.0 mm long (Figure 26–49B), and the latter is a pretty little black-and-white patterned species, 3–5 mm long (Figure 26–49A). Most damage done by these species is done by the larvae. The adults are often found on flowers.

This is one group of insects that every entomology student will encounter sooner or later. All the student has to do to get some dermestids is to make an insect collection and *not* protect it against these pests. The dermestids will eventually find the collection and ruin it. Many species in this group are serious pests in homes, markets, and food storage places.

This group contains one of the worst stored-products pests in the world, the khapra beetle, *Trogoderma granarium* Everts. A native of India, this beetle is frequently intercepted at ports of entry into this country, and in 1953 it became established in California, Arizona, and New Mexico. It is now apparently eradicated in the United States.

Although many of the dermestids are serious pests, they are nevertheless of value as scavengers, helping remove dead organic matter. Some species that feed on carrion, notably species of *Dermestes*, have been used by vertebrate zoologists to clean skeletons for study. One species in this family, *Thylodrias contractus* Motschulsky, is unusual in having filiform antennae and wingless and larviform females.

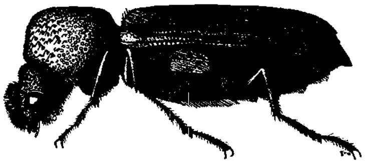

Figure 26–50 A bostrichid beetle, *Apate monacha* Fabricius. (Courtesy of Wolcott and the Journal of Agriculture of the University of Puerto Rico.)

Family **Bostrichidae—Branch and Twig Borers and Powderpost Beetles:** Most beetles in this group (more than 70 North American species) are elongate and somewhat cylindrical, and the head is bent down and scarcely visible from above (Figure 26–50), except for the Lyctinae. The antennae are straight, with a loose three- or four-merous club. Most species vary in length from 3.5 to 12.0 mm, but one western species, *Dinapate wrighti* Horn, which breeds in palms, reaches a length of 52 mm. Most species in this group are wood-boring and attack living trees, dead twigs and branches, or seasoned lumber. The apple twig borer, *Amphicerus bicaudatus* (Say), attacks the twigs of apple, pear, cherry, and other trees. *Rhizopertha dominica* (Fabricius), the lesser grain borer, is a major pest of stored grain worldwide.

One species in this family that occurs in the West, *Scobicia declivis* (LeConte), is rather unusual in that the adults would often bore into the lead sheathing once used to insulate telephone cables. This insect normally bores in the wood of oak, maple, and other trees. The beetles would make holes in the sheathing about 2.5 mm in diameter that allowed moisture to enter the cable, short-circuiting the wires and consequently interrupting service. This insect is commonly known as the "lead-cable borer" or "short-circuit beetle."

The bostrichids in the subfamily Psoinae, which occur principally in the West, differ from other bostrichids in that the head is large and easily visible from above, and the mandibles are large and strong. The members of the genus *Polycaon* are 14–28 mm long, are brown or black, and often greatly damage orchards in California and Oregon by severely pruning the trees. The larvae tunnel through the heartwood of these trees, but the adults seldom enter the wood. *Psoa maculata* (LeConte), 6 mm long, is the "spotted limb borer" of California. It breeds only in dead twigs of trees or shrubs and is usually bluish black or greenish with dense gray hair and with a few large, lighter spots on the elytra.

Members of the subfamily Lyctinae are known as "powderpost beetles" because they bore into dry and seasoned wood and reduce it to a powder. Species of *Lyctus* may completely destroy furniture, wooden beams (particularly in barns and cabins), tool handles, and hardwood floors. They live beneath the surface for months, and timbers from which the adults have emerged may be peppered with tiny holes, as though fine shot had been fired into them (Figure 26–51). These beetles do not enter wood that is painted or varnished. The powderpost beetles are slender and elongate (Figure 26–52B), uniformly colored brown to black, and 2–7 mm long; the head is prominent from

Figure 26–51 A board damaged by powderpost beetles, and showing exit holes of the beetles.

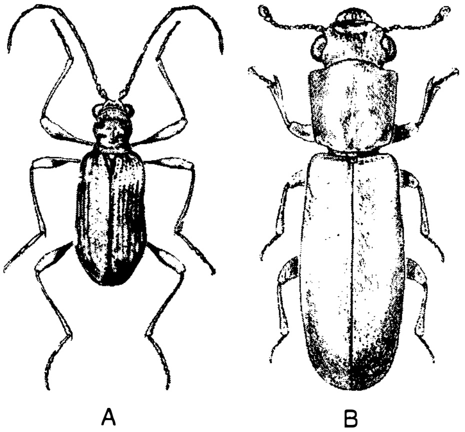

Figure 26–52 A, a spider beetle, *Ptinus fur* (L.), 5×; B, a powderpost beetle, *Trogoxylon parallelopipedum* (Melsheimer), 10×. (Courtesy of Arnett.)

above, and the antennae have a two-merous club. There are 11 species in North America.

***Family* Anobiidae—The Death Watch and Spider Beetles:** The anobiids are cylindrical to oval, pubescent beetles, 1–9 mm long. The head is deflexed and is usually concealed from above by the hoodlike pronotum. Most have the last three antennomeres enlarged and lengthened (Figures 26–5C and 26–53B,D–F). A few have these antennomeres lengthened but not enlarged, and a few have serrate or pectinate antennae. There are 464 species known from the Nearctic Region, including Mexico.

Most anobiids live in dry vegetable materials such as logs and twigs or under the bark of dead trees. Others pass the larval stage in fungi or in the seeds and stems of various plants. Some species, such as *Xestobium rufovillosum* (DeGeer) (Figure 26-53F), are called "death watch beetles" because they make a ticking sound as they bore through wood which is audible to the human ear when conditions are quiet (as at a wake).

Some of the anobiids are common and destructive pests. The drugstore beetle, *Stegobium paniceum* (L.) (Figure 26–53E), infests various drugs and cereals. The cigarette beetle, *Lasioderma serricorne* (Fabricius) (Figure 26–53C), is common in dried tobacco, museum specimens, insect collections, and various household products. In some parts of the United States, it is a

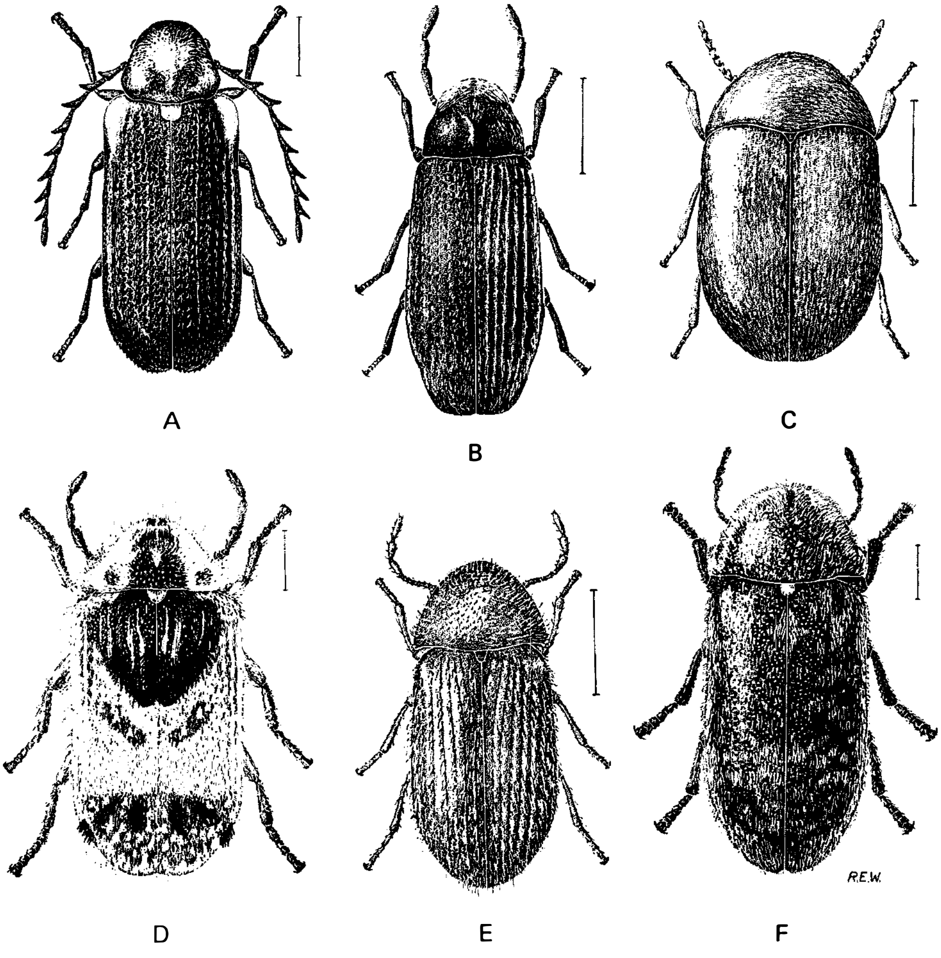

Figure 26–53 Anobiid beetles. A, *Eucrada humeralis* (Melsheimer); B, the furniture beetle, *Anobium punctatum* (De Geer); C, the cigarette beetle, *Lasioderma serricorne* (Fabricius); D, *Trichodesma gibbosa* (Say); E, the drugstore beetle, *Stegobium paniceum* (L.); F, a death watch beetle, *Xestobium rufovillosum* (De Geer). The lines represent 1 mm. (Courtesy of White and the Ohio Biological Survey.)

common household pest, infesting paprika, pepper, chili powder, pet foods, cereals, and other materials. Some wood-boring species, such as the furniture beetle, *Anobium punctatum* (DeGeer) (Figure 26–53B), bore in timbers, woodwork, and furniture; *Hemicoelus gibbicollis* (LeConte), the Pacific powderpost beetle, damages buildings along the Pacific Coast from California to Alaska, feeding chiefly in well-seasoned wood.

Spider beetles, subfamily Ptininae, are long-legged, 1–5 mm long, whose head and pronotum is much narrower than the elytra and appear somewhat spiderlike (Figure 26–52A). The head is nearly or completely concealed from above. Many species are minor pests of stored grain products. Some feed on both plant and animal products and attack museum specimens. One species passes its larval stages in rat droppings, and another (*Ptinus californicus* Pic) feeds on the pollen stored in nests of solitary bees. There are around 69 species of this subfamily in North America.

***Family* Lymexylidae—Ship-Timber Beetles:** This group is represented in the United States by two rare species that live under bark and in dead logs and stumps. They cause much of the pinhole damage in chestnut and oak. These beetles are long and narrow, and 9.0 to 13.5 mm long; the head is bent down and narrowed behind the eyes to form a short neck; the antennae are filiform to serrate; the tarsi are five-merous; and the maxillary palps in the males are long and flabellate. These beetles are called "ship-timber beetles" because one European species has been very destructive to ship timbers. One of the two North American species, *Elateroides lugubris* (Say), is commonly called the "sapwood timberworm"; it lives in fairly fresh poplar logs.

***Family* Trogossitidae—Bark-Gnawing Beetles, Cadelles:** This group (59 species in the United States and Canada) contains four subfamilies that differ rather markedly in shape. Members of the largest subfamily, Trogossitinae, are elongate, with the head about as wide as the pronotum and with the pronotum rather widely separated from the base of the elytra (Figure 26–54). The Peltinae are oval or elliptical, with the head only about half as wide as the pronotum, and the pronotum rather closely joined to the base of the elytra. The Peltinae are very similar to some nitidulids, but most species have long, erect hairs on the elytra, whereas the similarly shaped nitidulids have the elytra bare or with short pubescence. The Trogossitinae are chiefly predaceous on insects under bark, but the Peltinae feed chiefly on fungi.

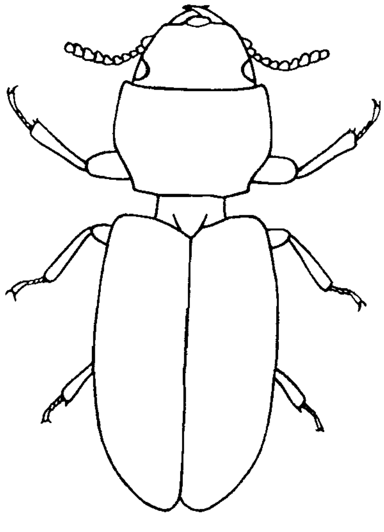

Figure 26–54 A trogossitid beetle, *Tenebrioides* sp., 7½×.

Trogossitids are 2.6 to 20.0 mm long, and most are brownish or blackish. A few are bluish or greenish. The cadelle, *Tenebroides mauritanicus* (L.) (Figure 26–54), lives commonly in granaries. It is believed to feed both on other insects in the grain and on the grain itself. *Temnochila virescens* (Fabricius), a rather common and widely distributed species, is a bright blue-green beetle about 20 mm long. It can bite viciously with its powerful mandibles. Adults and larvae of trogossitids are generally found under bark, in woody fungi, and in dry vegetable matter.

***Family* Cleridae—Checkered Beetles:** The clerids are elongate, very pubescent beetles 3–24 (mostly 5–12) mm long, and many are brightly colored. The pronotum is usually narrower than the base of the elytra and sometimes narrower than the head (Figure 26–55). The tarsi are five-merous, but in many species the first or the fourth tarsomere is very small and difficult to see. The antennae are usually clubbed, but are sometimes serrate, pectinate, or (rarely) filiform. There are 291 species of Cleridae in North America.

Most checkered beetles are predaceous as both adults and larvae. Many are common on or within tree trunks and logs, where they prey on the larvae of various wood-boring insects (chiefly bark beetles). Others live on flowers and foliage. A few (for example, *Trichodes*, Figure 26–55E) are pollen feeders in the adult stage and sometimes also in the larval stage. *Trichodes* larvae sometimes develop in the egg pods of grasshoppers or in the nests of bees and wasps.

Some authorities have placed some of the clerids, which have the fourth tarsomere very small and difficult to see, in a separate family, the Corynetidae. These beetles are similar in general appearance and habits to the other clerids. One species in this group, *Necrobia rufipes* DeGeer (Figure 26–55D), the red-

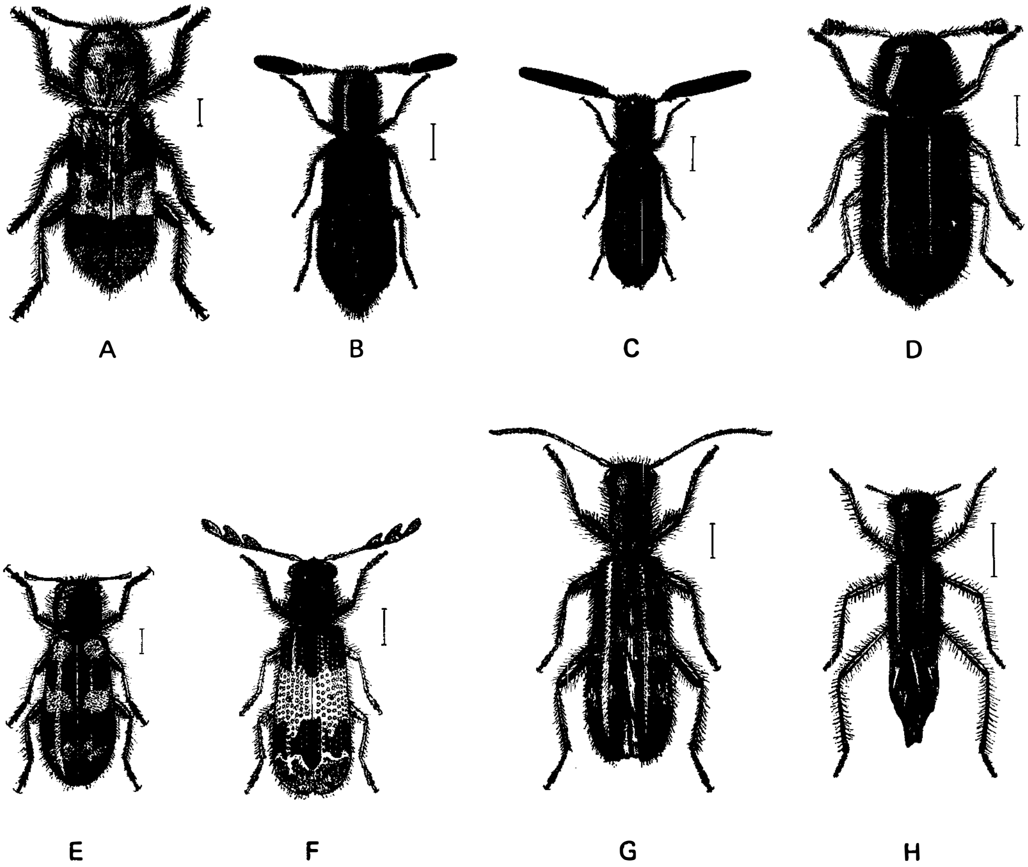

Figure 26–55 Checkered beetles. A, *Enoclerus ichneumoneus* (Fabricius); B, *Monophylla terminata* (Say), female; C, same, male; D, the red-legged ham beetle, *Necrobia rufipes* (De Geer); E, *Trichodes nuttalli* (Kirby); F, *Corinthiscus leucophaeus* (Klug); G, *Cymatodera undulata* (Say); H, *Isohydnocera curtipennis* (Newman). The lines represent 1 mm. (Courtesy of Knull and the Ohio Biological Survey.)

legged ham beetle, is occasionally destructive to stored meats.

***Family* Melyridae—Soft-Winged Flower Beetles:** The members of this family (520 species in 58 genera in North America) are elongate-oval, soft-bodied beetles 10 mm long or less. Many are brightly colored with brown or red and black (Figure 26–56A). Some melyrids (Malachiinae) have peculiar orange structures along the sides of the abdomen, which may be everted and saclike or withdrawn into the body and inconspicuous. Some melyrids have the two basal antennomeres greatly enlarged. Most adults and larvae are predaceous, but many are common on flowers. The most common North American species belong to the genus *Collops* (Malachiinae); *C. quadrimaculatus* (Fabricius) is reddish, with two bluish black spots on each elytron.

***Family* Sphindidae—Dry-Fungus Beetles:** The sphindids are broadly oval to oblong, convex, dark brown to black beetles, 1.5 to 3.0 mm long. They have a 5-5-4 tarsal formula, and the 10-merous antennae terminate in a two- or three-merous club. The sphindids live in slime molds on dead trees, logs, and stumps and on dry fungi, such as the shelf fungi on tree trunks. Nine relatively rare species occur in the United States.

***Family* Brachypteridae—Short-winged Flower Beetles:** This small family (11 species in United States and Canada) was formerly treated as a subfamily of Nitidulidae, some members of which they resemble. The pygidium is exposed, the labial palps are not articulated, and the three-merous antennal club is not well defined. Larvae develop in seed capsules of various

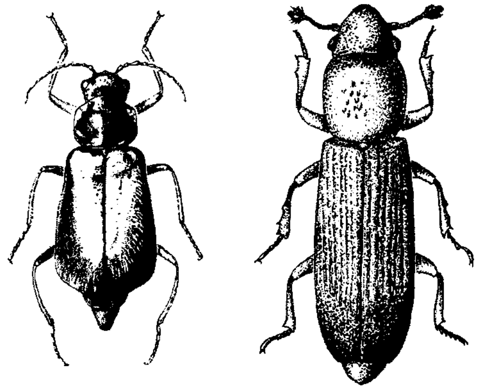

Figure 26–56 A, a soft-winged flower beetle, *Malachius aeneus* (L.) (Melyridae), 5×; B, a root-eating beetle, *Rhizophagus bipunctatus* (Say) (Monotomidae), 18×. (Courtesy of Arnett.)

plants, and the adults feed on pollen and flower petals of some of the same plants.

Family **Nitidulidae—Sap Beetles:** The members of this family (about 165 North American species) vary considerably in size, shape, and habits. Most are small, 12 mm long or less, and elongate or oval, and in many the elytra are short and expose the terminal abdominal segment (Figure 26–57). The antennae usually have a three-merous club, but some have an annulated terminal antennomere, causing the club to appear four-merous (Figure 26–57B,C). Most nitidulids are found where plant fluids are fermenting or souring—for example, around decaying fruits or melons, flowing sap, and some types of fungi. A few live on or near the dried carcasses or dead animals, and several live in flowers. Others are very common beneath the loose bark of dead stumps and logs, especially if these are damp enough to be moldy.

Two members of the genus *Glischrochilus*, *G. quadrisignatus* (Say) and *G. fasciatus* (Oliver), both shiny black with two yellowish spots on each elytron, are called "picnic beetles." They frequently become so abundant at such affairs that, although they cause no damage, people are driven indoors. *Carpophilus lugubris* Murray (Figure 26–57B), the dusky sap beetle, is a serious pest of sweet corn, especially corn grown for canning. The larvae feed inside the kernels at the tip of the ear and are frequently overlooked during the canning operation.

Family **Smicripidae—Palmetto Beetles:** Members of this family closely resemble some of the Nitidulidae and were previously placed in that family. The truncate elytra, leaving two abdominal tergites exposed; a free and prominent labrum; and short, broadly triangular mandibles are characteristic. The tarsal formula may be either 4-4-4 or 5-5-5. Two species of *Smicrips* represent this family in North America. Both adults and larvae have been found in decaying vegetation, leaf litter, and under bark.

Family **Monotomidae—Root-Eating Beetles:** These beetles are small, slender, dark-colored, and 1.5 to 3.0 mm long (Figure 26–56B). They usually live under bark or in rotten wood. A few species live in ant nests, and some live in bark beetle galleries, where they feed on the eggs and young of bark beetles. The antennae are 10-merous with a 1- or 2-merous club; the last tarsomere is elongate and the other tarsomeres are short; the tip of the abdomen is exposed beyond the elytra;

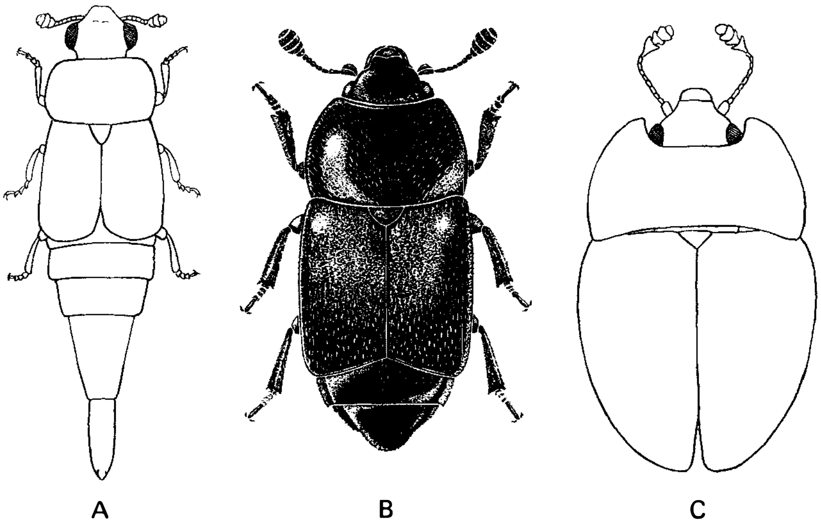

Figure 26–57 Representative Nitidulidae. A, *Conotelus obscurus* Erichson, 15×; B, *Carpophilus lugubris* (Murray), the dusky sap beetle, 15×; C, *Lobiopa* sp., 7½×.

and the first and fifth abdominal sterna are longer than the others. Fifty-five species occur in North America.

***Family* Silvanidae:** Members of this family resemble cucujids and were previously placed in that family. They have long, slender, sometimes capitate antennae, and the head is constricted behind the eyes. The tarsal formula is 5-5-5. Although the group is mainly tropical, there are 32 species in 14 genera in North America. Most species appear to be fungivorous, and several are important pests of cereal products, including the saw-toothed grain beetles (*Oryzaephilus*, Figure 26–58B) and the foreign grain beetle, *Ahasverus advena* (Waltl).

***Family* Passandridae—Parasitic Flat Bark Beetles:** This family was formerly regarded as a subfamily of Cucujidae. They resemble cucujids, but the confluence of the gular sutures, expanded genae, and stout moniliform antennae will separate this small family from other flat beetles. There are three widespread species in two genera in North America.

***Family* Cucujidae—Flat Bark Beetles:** Most beetles in this group (three North American species in two genera), are extremely flat and are either reddish, brownish, or yellowish. Cucujids are found under the bark of freshly cut logs, chiefly maple, beech, elm, ash, and poplar. The only North American species of *Cucujus*, *C. clavipes* Fabricius, is uniform red and about 13 mm long (Figure 26–58A).

***Family* Laemophloeidae—Lined Flat Bark Beetles:** These beetles are very flat with distinctive sublateral lines on the head pronotum, and elytra; and with long, slender antennae. They were formerly considered a subfamily of Cucujidae, which they closely resemble. Several species of the genus *Cryptolestes* are minor pests of stored grain products, and some are thought to be predaceous. There are 52 species in 13 genera in the United States. The family is mainly tropical in distribution.

***Family* Phalacridae—Shining Flower Beetles:** The phalacrids are oval, shining, convex beetles, 1–3 mm long, with clubbed antennae (Figure 26–59A) and usually brownish. The pollen-feeding adults are sometimes quite common on the flowers of goldenrod and other composites. The larvae feed on fungus spores. About 122 species occur in North America.

***Family* Cryptophagidae—Silken Fungus Beetles:** These beetles (145 species in North America) are 1–5 mm long, elongate-oval in shape, yellowish brown, and covered with a silky pubescence. They feed on fungi, decaying vegetation, and similar materials and usually live in decaying vegetable matter. Some species live in nests of wasps or bumble bees.

***Family* Languriidae—Lizard Beetles:** The lizard beetles are narrow and elongate, 2–10 mm long, and usually have a reddish pronotum and black elytra (Figure 26–58D). The tarsi are 5-5-5, with the fourth tarsomere very small and tarsomeres 1–3 densely pubescent beneath. The antennae are 11-merous with a 3- to 6-merous club. The adults feed on the leaves and pollen of many common plants, including goldenrod, ragweed, fleabane, and clover. The larvae are stem bor-

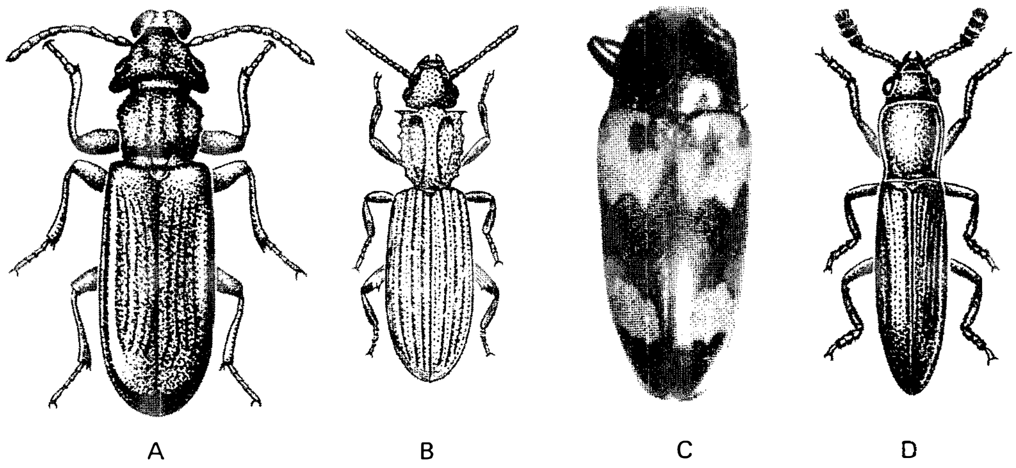

Figure 26–58 A, a flat bark beetle, *Cucujus clavipes* Fabricius (Cucujidae), 4×; B, the saw-toothed grain beetle, *Oryzaephilus surinamensis* (L.) (Silvanidae), 17×; C, a pleasing fungus beetle, *Megalodacne heros* (Say) (Erotylidae), 2½×; D, adult of the clover stem borer, *Languria mozardi* Latreille (Languriidae), 6×. (A, courtesy of Arnett; B, and D, courtesy of USDA; C, courtesy of Dwight M. DeLong.)

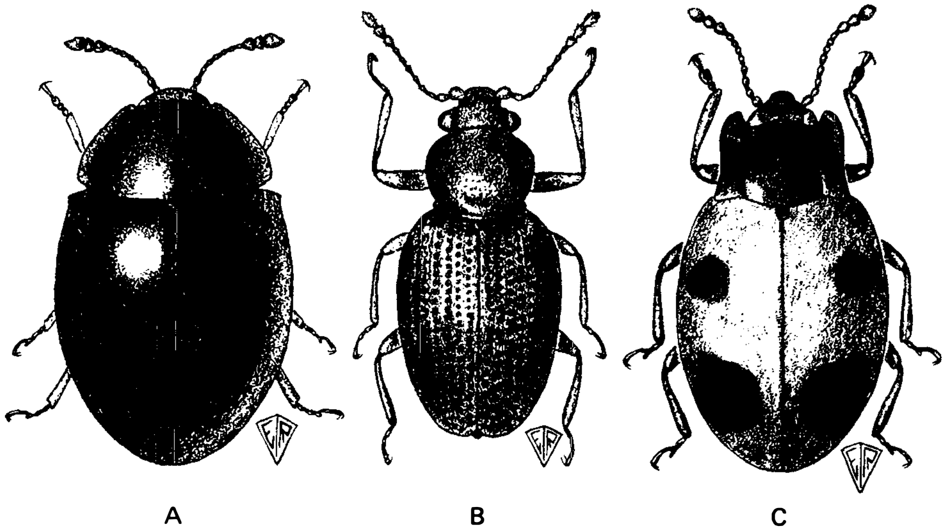

Figure 26–59 A, a shining flower beetle, *Phalacrus politus* Melsheimer (Phalacridae), 25×; B, a minute brown scavenger beetle, *Melanophthalma americana* Mannerheim (Latridiidae), 26×; C, a handsome fungus beetle, *Endomychus biguttatus* Say (Endomychidae), 12½×. (Courtesy of Arnett.)

ers; the larvae of the clover stem borer (*Languria mozardi* Latreille) attack clover and sometimes cause considerable damage. There are 33 species in North America.

Family **Erotylidae—Pleasing Fungus Beetles:** The erotylids are small to medium-sized, oval, and usually shiny beetles that are found on fungi or may be attracted to sap. They often live beneath the bark of dead stumps, especially where rotting fungus abounds. Some of the erotylids are brightly patterned with orange or red and black. The species in this group that have the tarsi distinctly five-merous are by some authorities placed in a separate family, the Dacnidae. The largest species of dacnids (*Megalodacne*) are about 20 mm long and are black, with two orange-red bands across the elytra (Figure 26–58C). In other erotylids the fourth tarsomere is very small, so that the tarsi appear four-merous. These beetles are smaller, 8 mm long or less. There are about 50 North American species, and some are fairly common insects.

Family **Byturidae—Fruitworm Beetles:** The byturids are small, oval, hairy beetles, pale brown to orange and mostly 3.5–4.5 mm long, with clubbed antennae (Figure 26–60B). The second and third tarsomeres are lobed beneath. The group is a small one, with only two

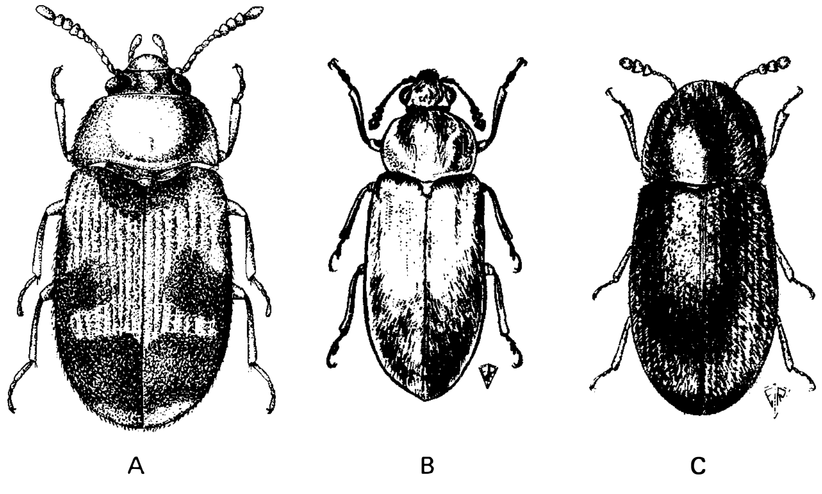

Figure 26–60 A, a hairy fungus beetle, *Mycetophagus punctatus* Say (Mycetophagidae), 8×; B, a fruitworm beetle, *Byturus bakeri* Barber (Byturidae), 8×; C, a minute tree-fungus beetle, *Cis fuscipes* Mellie (Ciidae), 14×. (Courtesy of Arnett.)

species in the United States. The only common eastern species is *Byturus unicolor* Say, a reddish yellow to blackish beetle 3.5 to 4.5 mm long that feeds on the flowers of raspberry and blackberry. The larva, called the "raspberry fruitworm," sometimes seriously damages berries.

Family **Biphyllidae—False Skin Beetles:** This family is closely related to Byturidae. The adults have slender tarsal lobes on tarsomeres two and three, closed procoxal cavities, and lateral lines on the first abdominal sternite. They live under bark and apparently feed on fungi. Three species in two genera, *Anchorius* and *Diplocoelus*, are known from the United States.

Family **Bothrideridae:** These beetles were previously placed in the Colydiidae. Most are long and slender, with a distinct antennal club and 4-4-4 tarsal formula. The antennal insertions are exposed, and the trochanters are greatly reduced so that the femur and coxa are in contact or nearly so. Many species are predators on wood-boring beetles and others feed on fungi. There are 18 species in eight genera in North America.

Family **Cerylonidae—Minute Bark Beetles:** This family includes a group of genera formerly placed in the Colydiidae (*Cerylon, Philothermus, Euxestus*, and five genera in the subfamily Murmidiinae). They are somewhat more oval and flattened than most colydiids and 2–3 mm long. The antennae are 10-merous with an abrupt 1- or 2-merous club and are received in a cavity of the prothorax, and the coxae are widely separated. They are unusual in having piercing-sucking mouthparts in the larval stage and in some adults. The 19 North American species in this group are widely distributed. *Cerylon castaneum* Say is fairly common under dead bark, but the other species are relatively rare.

Family **Endomychidae—Handsome Fungus Beetles:** These are small, oval beetles, mostly 3–8 mm long. They are smooth and shiny and usually brightly colored. They are somewhat similar to the Coccinellidae, but the head is easily visible from above. The pronotum is broadly excavated or grooved laterally, with the sides produced forward (Figure 26–59C), and the pretarsal claws are simple. Some members of this group (the Mycetaeinae, with 15 North American species) have the tarsi appearing four-merous, with the third tarsomere easily visible. The others (28 North American species, in four subfamilies) have the third tarsomere very small, and the tarsi appear three-merous. Most endomychids live under bark, in rotting wood, in fungi, or in decaying fruits and feed on fungus and mold. A few of the Mycetaeinae are found on flowers. One species, *Mycetaea subterranea* (Fabricius), is occasionally a pest in granaries and warehouses, because it spreads mold infection.

Family **Coccinellidae—Ladybird Beetles:** The ladybird beetles (ladybugs) are a well-known group of small (0.8–10 mm long), oval, convex, and often brightly colored insects containing about 475 North American species in 57 genera. The head is concealed from above by the expanded pronotum. They may be distinguished from the chrysomelids, many of which have a similar shape, by the three distinct tarsomeres (chrysomelids appear to have four tarsomeres). Most ladybird beetles are predaceous, as both larvae and adults, and feed chiefly on aphids. They are frequently quite common, particularly on vegetation where aphids are numerous. Ladybirds hibernate as adults, frequently in large aggregations, under leaves or in debris. The multicolored Asian ladybird beetle, *Harmonia axyidris* (Pallas), is an introduced species that feeds on aphids and mealybugs. It has attained enormous populations and often becomes a nuisance pest by entering buildings during cold weather.

The larvae of ladybird beetles (Figure 26–61C) are elongate, somewhat flattened, and covered with minute tubercles or spines. They are usually spotted or banded

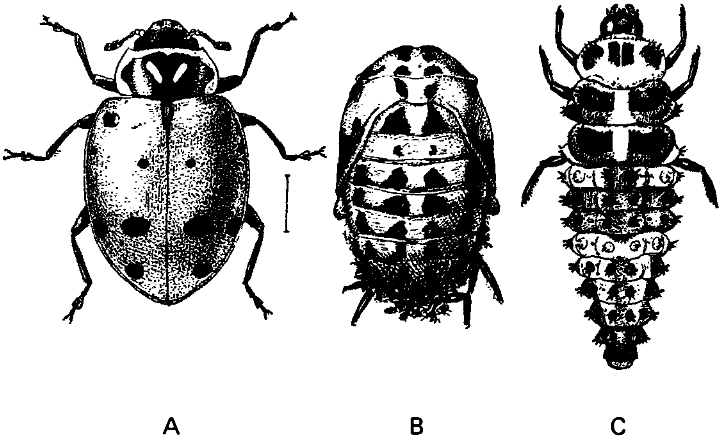

Figure 26–61 A ladybird beetle, *Hippodamia convergens* Guérin-Méneville. A, adult; B, pupa; C, larva. The line at the right of the adult indicates the actual size. (Courtesy of USDA.)

with bright colors. These larvae are often found in aphid colonies.

Two fairly common phytophagous species in this group are serious garden pests: the Mexican bean beetle, *Epilachna varivestis* Mulsant, and the squash beetle, *E. borealis* (Fabricius). The Mexican bean beetle is yellowish, with eight spots on each elytron. The squash beetle is pale orange-yellow, with three spots on the pronotum and a dozen or so large spots arranged in two rows on the elytra, plus a large black dot near the tip of the elytra. These two species are the only large ladybird beetles in the United States that are pubescent. The larvae of these species are yellow and oval in shape, with forked spines on the body. Both larvae and adults are phytophagous, and they are often very destructive.

Except for the two species of *Epilachna*, the ladybird beetles are a very beneficial group of insects. They feed on aphids, scale insects, and other injurious insects and mites. During serious outbreaks of aphids or scale insects, large numbers of ladybird beetles are sometimes imported into the infested areas to serve as a means of control. The cottony cushion scale, *Icerya purchasi* Maskell, a pest of citrus in California, has been kept under control for a number of years by means of a ladybird beetle, *Rodolia cardinalis* (Mulsant), imported from Australia.

***Family* Corylophidae—Minute Fungus Beetles:** These beetles are rounded or oval and generally less than 1 mm long. The tarsi are four-merous, but the third tarsomere is small and concealed in a notch of the bilobed third tarsomere, and the tarsi appear three-merous. The antennae are clubbed, and the club is usually three-merous. The hind wings are fringed with hairs. These beetles live in decaying vegetable matter and in debris, where they apparently feed on fungus spores. Sixty-one species occur in North America.

***Family* Latridiidae—Minute Brown Scavenger Beetles:** The latridiids (140 North American species) are elongate-oval, reddish brown beetles, 1–3 mm long (Figure 26–59B). The pronotum is narrower than the elytra, and each elytron bears six or eight rows of punctures. The tarsi are three-merous (Figure 26–101) or (males) 2-3-3 or 2-2-3. These beetles are found in moldy material (including stored food products) and debris and sometimes on flowers.

***Family* Mycetophagidae—Hairy Fungus Beetles:** The mycetophagids are broadly oval, flattened, rather hairy beetles, 1.5–5.5 mm long (Figure 26–60A). They are brown to black and often brightly marked with reddish or orange. These beetles live under bark, in shelf fungi, and in moldy vegetable material. There are 26 species of mycetophagids in North America. *Typhaea stercorea* (L.), the hairy fungus beetle, is a fairly common pest in stored products.

***Family* Archeocrypticidae:** This family is very similar to Tenebrionidae, with which it was historically associated. The main character separating them from tenebrionids is the lateral posterior extensions of the prosternal process that partially closes the procoxal cavities. The family is mainly pantropical, with one species, *Enneboeus caseyi* Kaszab, occurring in the southeastern United States south into Central America.

***Family* Ciidae—Minute Tree Fungus Beetles:** The ciids (Figure 26–60C) are brownish to black beetles, 0.5 to 6.0 mm long, and similar in appearance to the bark beetles (Curculionidae: Scolytinae), and Bostrichidae. The body is cylindrical; the head is deflexed and not visible from above; the tarsi are four-merous (with the first three tarsomeres short and the fourth long); the antennae terminate in a three-merous club; and sexual dimorphism is usually evident. These beetles (84 species in North America) live under bark, in rotting wood, or in dry woody fungi, often in considerable numbers. They feed on fungi.

***Family* Tetratomidae—Polypore Fungus Beetles:** Members of this family were formerly associated with the Melandryidae. The pubescent body, relatively large, emarginate compound eyes, and front coxae separated by a prosternal process characterize this small family (26 species in 10 genera in the United States). Most feed on fungi or under fungus-grown bark. The most common tetratomids are the oval, black, eastern members of *Penthe*, which are 5–15 mm long and common under old, dead bark: *P. pimelia* (Fabricius) is entirely black, and *P. obliquata* (Fabricius) has a bright orange scutellum.

***Family* Melandryidae—False Darkling Beetles:** The members of this group (60 North American species in 24 genera) are elongate-oval, somewhat flattened beetles usually found under bark or logs. Some species live on flowers and foliage, others in fungi. They are mostly dark-colored and 3–20 mm long. They can usually be recognized by the 5-5-4 tarsal formula, the open front coxal cavities, and the two impressions near the posterior border of the pronotum (Figure 26–62A).

***Family* Mordellidae—Tumbling Flower Beetles:** These beetles have a rather characteristic body shape (Figure 26–63): the body is somewhat wedge-shaped and humpbacked, the head is bent down, and the abdomen is pointed apically and extends beyond the tips of the elytra. Most mordellids (more than 200 North American species) are black or mottled gray, and the body is covered with a dense pubescence. Most are 3–7 mm long, but some reach 14 mm. These beetles are common on flowers, especially the composites. They are quite active and run or fly quickly when disturbed. Their common name is derived from the tumbling movements they make in attempting to escape capture. The larvae live in decaying wood and in plant pith. Some are predaceous.

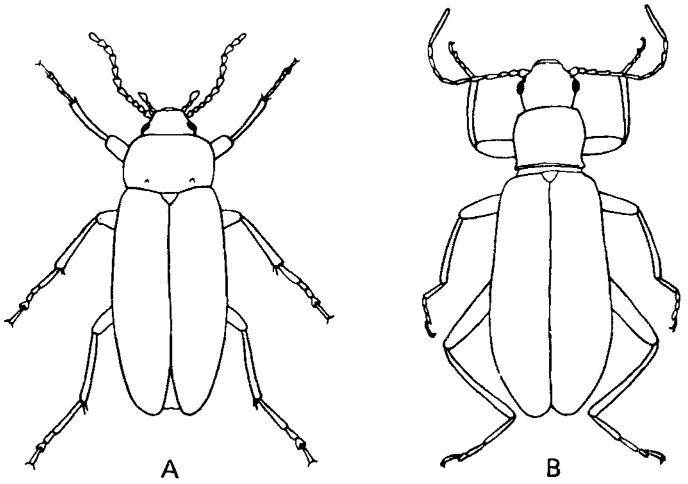

Figure 26–62 A, *Emmesa labiata* (Say) (Melandryidae); B, *Arthromacra* sp. (Tenebrionidae, Lagriinae); 4×.

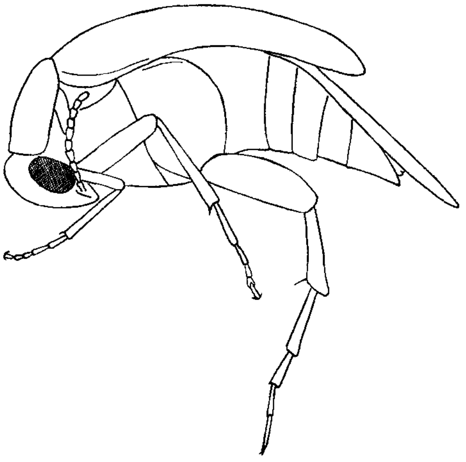

Figure 26–63 A tumbling flower beetle, *Mordella marginata* Melsheimer, 15×.

Family **Ripiphoridae—Wedge-Shaped Beetles:** These beetles, 4–15 mm long, are similar to the Mordellidae, but have the abdomen blunt instead of pointed at the apex. The elytra are more or less pointed apically and usually do not cover the tip of the abdomen. In some species the elytra are quite short. The antennae are pectinate in the males and serrate in the females. Adult beetles feed on flowers, particularly goldenrod, but they are not very common. They are sometimes found in the burrows of halictid bees. The larval stages are parasitic on various wasps (Vespidae, Scoliidae, and Tiphiidae) and bees (Halictidae and Apidae). They undergo hypermetamorphosis similar to that in the Meloidae. Some females in this family are wingless and larviform. There are 51 North American species.

Family **Colydiidae—Cylindrical Bark Beetles:** The colydiids are hard-bodied, shiny beetles, 1–8 mm long. Some species are oval or oblong and slightly flattened, and some are elongate and cylindrical. The antennae are 10- or 11-merous and terminate in a 2- or 3-merous club, and the tarsi are 4-merous. These beetles live under dead bark, in shelf fungi, or in ant nests. Many species are predaceous, others are plant feeders, and a few species (in the larval stage) are ectoparasites of the larvae and pupae of various wood-boring beetles. There are 73 species in North America.

Family **Monommatidae:** The monommatids (Figure 26–64A) are black oval beetles, 5–12 mm long, and are flattened ventrally and convex dorsally. They have a 5-5-4 tarsal formula, with the first tarsomere relatively long. The anterior coxal cavities are open behind, the legs are strongly retractile, and the antennae terminate in a two- or three-merous club and are received in grooves on the underside of the prothorax. The adults are found in leaf litter, and the larvae live in rotten wood. The group is a small one, with the six species occurring in the southern states, from Florida to southern California.

Family **Zopheridae—Ironclad Beetles:** This family as now constituted contains elements previously placed in Tenebrionidae and Colydiidae. The larger ones have an extremely hard integument and are difficult to pin, hence the common name. The antennae are short and stout, and the procoxal cavities are open. There are nine genera with about 30 species in the United States, 19 in the genus *Zopherus*. All are western except *Phellopsis obcordata* (Kirby), which occurs in New England, Tennessee, and Virginia on shelf fungi.

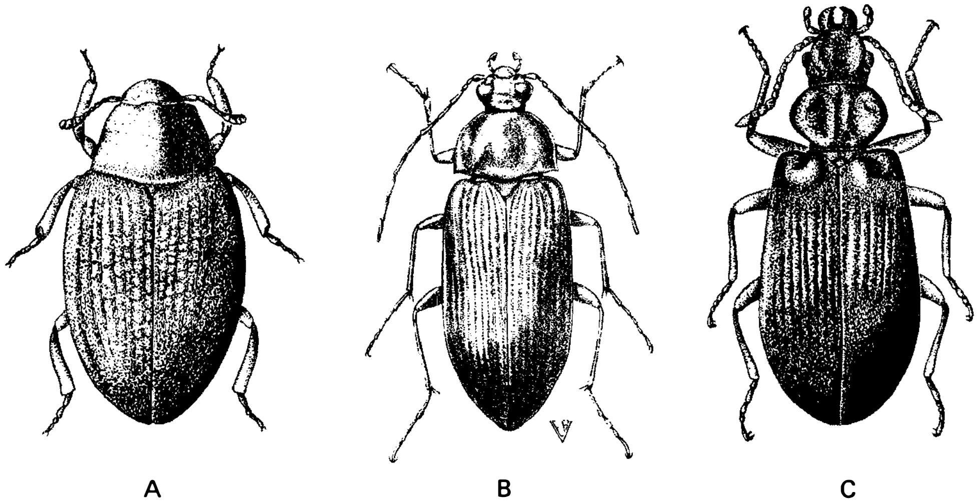

Figure 26–64 A, a monommatid beetle, *Hypophagus opuntiae* Horn, 3½×; B, a comb-clawed beetle, *Capnochroa fuliginosa* (Melsheimer) (Tenebrionidae, Alleculinae), 4½×; C, a narrow-waisted bark beetle, *Pytho niger* Kirby (Pythidae), 4×. (Courtesy of Arnett.)

Family **Tenebrionidae—Darkling Beetles:** The tenebrionids are a large and varied group, but can be distinguished by the 5-5-4 tarsal formula; the front coxal cavities closed behind (Figure 26–7B); the eyes usually notched; the antennae nearly always 11-merous and either filiform or moniliform; and five visible abdominal sterna. Most tenebrionids are black or brownish (Figure 26–65), but a few, for example, *Diaperis* (Figure 26–65B), have red markings on the elytra. Many are black and smooth and resemble ground beetles. Some of the species that feed on the bracket fungi are brownish and rough-bodied and resemble bits of bark. One such species, *Bolitotherus cornutus* (Panzer), has two hornlike protuberances extending forward from the pronotum (Figure 26–65I). The fungus-inhibiting members of the genus *Diaperis* are somewhat similar in general appearance to the ladybird beetles (Figure 26–65B). Some of the tenebrionids are very hard-bodied.

Throughout the arid regions of the United States, these beetles take over the ecological niche occupied by the Carabidae in more verdant areas, being very common under stones and rubbish and beneath loose bark, and even being attracted to lights at night.

The most distinctive habit of the members of the extremely large genus *Eleodes* (Figure 26–65G) is the ridiculous position they assume when running from possible danger: The tip of the abdomen is elevated to an angle of about 45 degrees from the ground, and the beetles almost seem to be standing on their head as they run. When disturbed or picked up, they emit a reddish black fluid with a very disagreeable odor.

Most tenebrionids feed on plant materials of some sort. A few are common pests of stored grain and flour and are often very destructive. The beetles in the genus *Tenebrio* are black or dark brown and 13–17 mm long, and they feed on grain products in both larval and adult stages. The larvae are commonly called "mealworms" and are quite similar to wireworms. The members of the genus *Tribolium* are oblong brown beetles, 5 mm or less in length (Figure 26–65E). Both adults and larvae commonly live in flour, cornmeal, dog food, cereals, dried fruits, and similar materials.

The members of the subfamily Alleculinae, the comb-clawed beetles, are small, 5-15 mm long, elongate-oval, and usually brownish or black with a somewhat glossy or shiny appearance resulting from the pubescence on the body (Figure 26–64B). They can be distinguished by the pectinate pretarsal claws (Figure 26–11B). The adults are found on flowers and foliage, on fungi, and under dead bark. The larvae resemble wireworms and live in rotting wood, plant debris, or fungi.

The Lagriinae are slender beetles that can usually be recognized by their characteristic shape (Figure 26–62B) and the elongate apical antennomere (Figure 26–5D). They are 10–15 mm long and dark metallic. The adults are found on foliage or occasionally under bark. The larvae breed in plant debris and under the bark of fallen trees.

The Tenebrionidae is the fifth largest family of beetles, with upward of 1000 North American species, and many of its members are common insects. Most North American species are western.

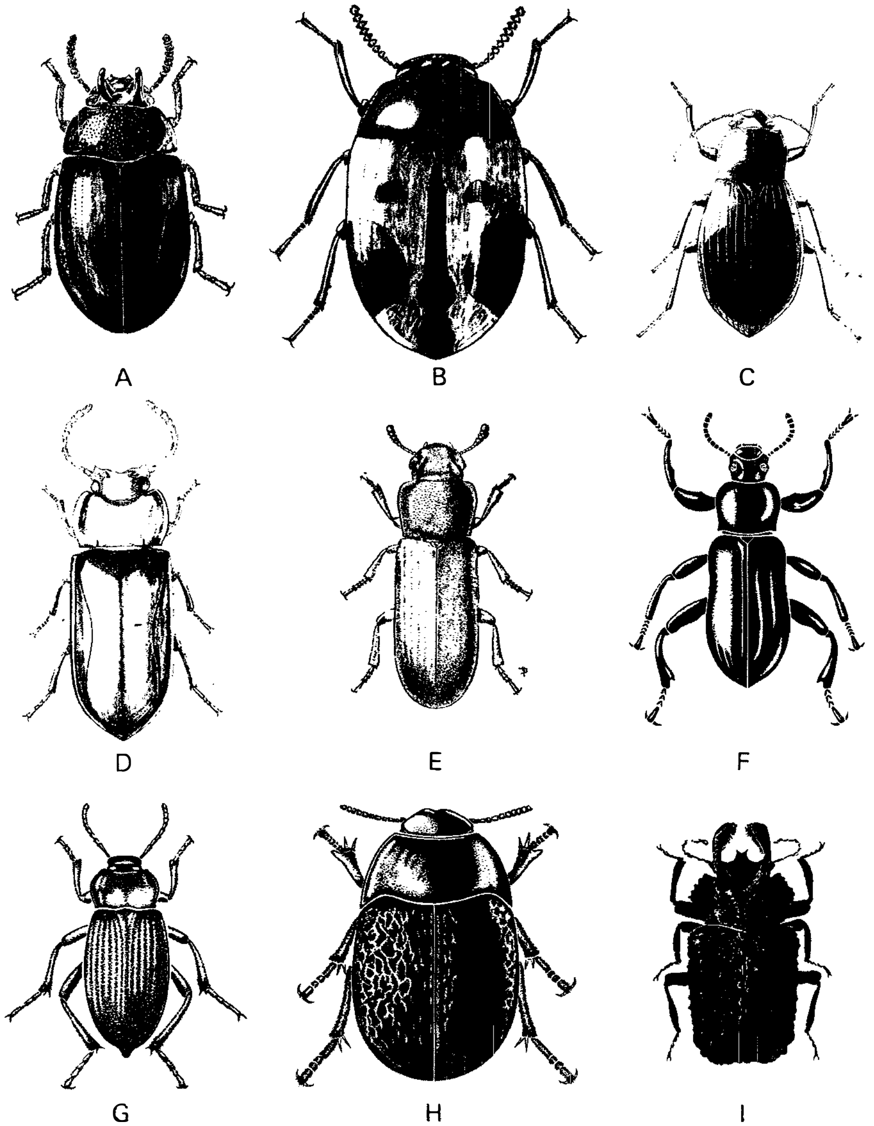

Figure 26–65 Darkling beetles (Tenebrionidae). A, *Neomida bicornis* (Fabricius), 8×; B, *Diaperis maculata* (Olivier), 6×; C, *Helops aereus* Germar, 4×; D, *Adelina plana* (Say), 7×; E, the confused flour beetle, *Tribolium confusum* du Val, 10×; F, *Merinus laevis* (Oliver), 1½×; G, *Eleodes suturalis* (Say), 0.75×; H, *Eusattus pons* Triplehorn, 3×; I, *Bolitotherus cornutus* (Panzer), male, 3×. (E, courtesy of USDA; I, courtesy of Liles.)

Family **Prostomidae—Jugular-Horned Beetles:** Only one species of this family, *Prostomis mandibularis* (Fabricius) is found in North America. It had been placed in Cucujidae and is separated largely by larval characters. A distinguishing feature is its rather large head with prominent, projecting, stout mandibles. The larvae and adults are associated with dead wood.

Family **Synchroidae:** These beetles superficially resemble click beetles (Elateridae) in shape, but are heteromerous and have open fore coxal cavities. They were previously placed in Melandryidae. Adults and larvae are found in decaying wood and under bark, where they feed on fungi. There are two genera, *Synchroa* and *Mallodrya*, each with one species in eastern North America.

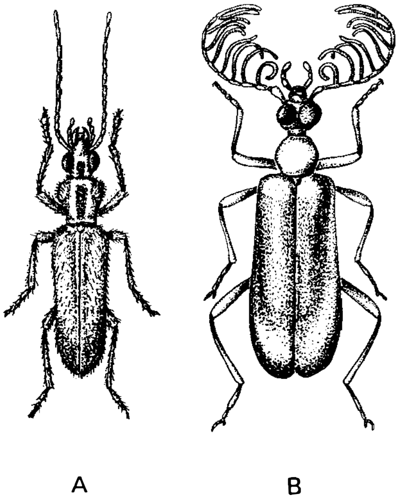

Figure 26–66 A, a false blister beetle, *Oxacis trimaculata* Champion (Oedemeridae), 3×; B, a fire-colored beetle, *Dendroides canadensis* LeConte (Pyrochroidae), 3×. (Courtesy of Arnett.)

***Family* Oedemeridae—False Blister Beetles:** The oedemerids are slender, soft-bodied beetles, 5–20 mm long (Figure 26–66A). Many are black with an orange pronotum, whereas others are pale with blue, yellow, red, or orange markings. These beetles have a 5-5-4 tarsal formula, and the penultimate tarsomere is dilated and densely hairy beneath (Figure 26–10C). The pronotum is anteriorly broadened and posteriorly narrower than the base of the elytra, and the eyes are often emarginate. The adults are usually found on flowers or foliage and are attracted to lights at night. The larvae live in moist, decaying wood, especially driftwood. The larvae of the wharf borer, *Nacerdes melanura* (L.), feed in very moist wood such as pilings under wharves, under buildings near water, and in greenhouses; the adult is 7–15 mm long and reddish yellow with the tips of the elytra black. There are 87 species in the United States and Canada.

***Family* Stenotrachelidae—False Longhorn Beetles:** These beetles are elongate, convex, and somewhat similar to a cerambycid in shape (hence the common name). They are brownish to dark and 8–20 mm long, and the head is somewhat diamond-shaped, narrowed behind the eyes to form a slender neck. They have a 5-5-4 tarsal formula, the pretarsal claws (of 6 of our 10 species) are pectinate, and there is a long (broad to narrow) pad under each claw. Little is known of the habits of these beetles, except that the adults are sometimes found on flowers and the larvae have been found in very old rotten logs. Ten species are known from the United States.

***Family* Meloidae—Blister Beetles:** The blister beetles (more than 400 North American species) are usually narrow and elongate; the elytra are soft and flexible; and the pronotum is narrower than either the head or the elytra (Figure 26–67). These beetles are called "blister beetles" because the body fluids of the commoner species contain cantharadin, a substance that often causes blisters when applied to the skin.

Several species of blister beetles are important pests, feeding on potatoes, tomatoes, and other plants. Two of these are often called the "old-fashioned potato beetles": *Epicauta vittata* (Fabricius) (with orange and black longitudinal stripes) and *Epicauta pestifera* Werner (black, with the margins of the elytra and the sutural stripe gray; Figure 26–67C). These beetles are 12–20 mm long. The black blister beetle, *E. pennsylvanica* (DeGeer), is a common black meloid, 7–13 mm long, that is usually found on the flowers of goldenrod.

The larvae of many blister beetles are considered beneficial, because they feed on grasshopper eggs. A few live in bee nests in the larval stage, where they feed on bee eggs and on the food stored in the cells with the eggs.

The life history of the blister beetles in the genus *Epicauta* is rather complex. These insects undergo hypermetamorphosis, with the different larval instars being quite different in form (Figure 26–68). The first larval instar, an active, long-legged form called a *triungulin*, seeks out a grasshopper egg or a bee nest and then molts. In the species that develop in bee nests, the triungulin usually climbs on a flower and attaches itself to a bee that visits the flower. The bee carries the triungulin to the nest, whereupon the triungulin attacks the bee's eggs. The second instar is somewhat similar to the triungulin, but the legs are shorter. In the third, fourth, and fifth instars, the larva becomes thicker and somewhat scarabaeiform. The sixth instar has a darker and thicker exoskeleton and lacks functional appendages. This instar is usually known as the *coarctate larva* or *pseudopupa*, and it is the instar that hibernates. The seventh instar is small, white, and active (though legless) but apparently does not feed and soon transforms to the true pupa.

The members of the genus *Meloe*, some of which are about 25 mm long, have very short elytra that overlap just behind the scutellum, and they lack hind wings. These insects are dark blue or black (Figure 26–67A). They are sometimes called "oil beetles," because they often exude an oily substance from the joints of the legs when disturbed.

The blister beetles in the genus *Nemognatha* are unique in having the galeae prolonged into a sucking tube as long as or longer than the body. These beetles are usually brownish (sometimes blackish, or brown and black) and 8–15 mm long. They are widely distributed.

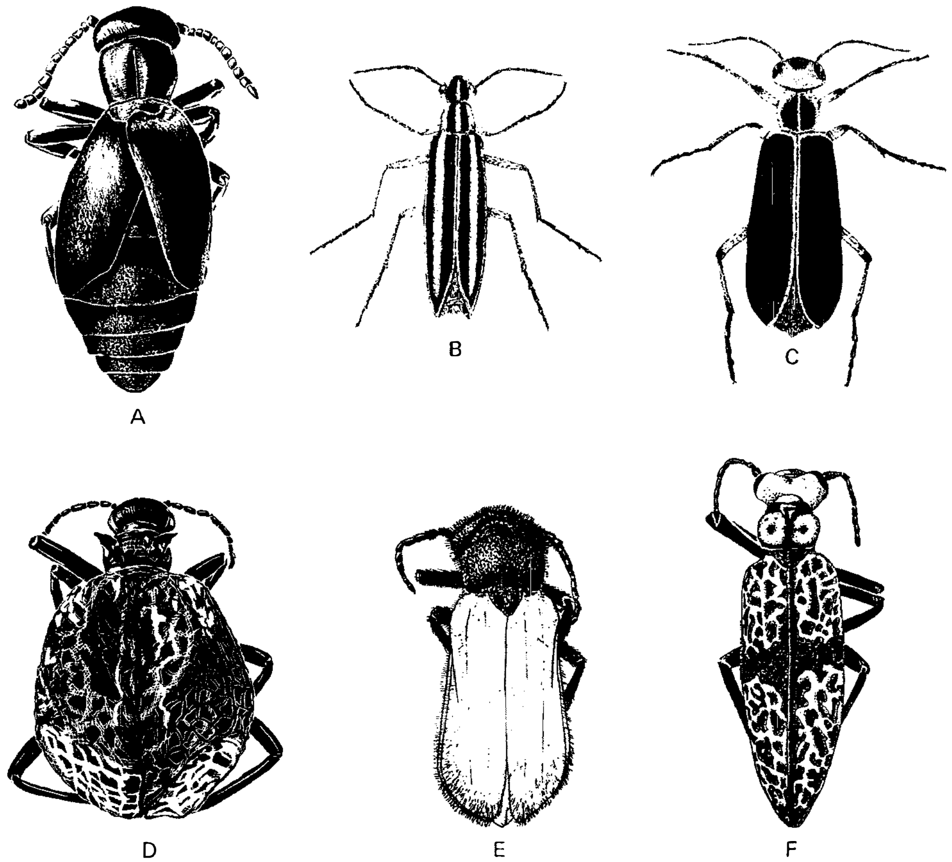

Figure 26–67 Blister beetles. A, *Meloe laevis* Leach, 2×; **B**, the three-striped blister beetle, *Epicauta lemniscata* (Fabricius), 2×; C, *Epicauta pestifera* Werner, 2×; D, *Cysteodemus armatus* LeConte, 2½×; E, *Tricrania stansburyi* (Haldeman), 4×; F, *Tegrodera erosa aloga* (Skinner), 2×. (**B**, and **C**, courtesy of Baerg and the Arkansas Agricultural Experiment Station; others, courtesy of Noller and the Arizona Agricultural Experiment Station.)

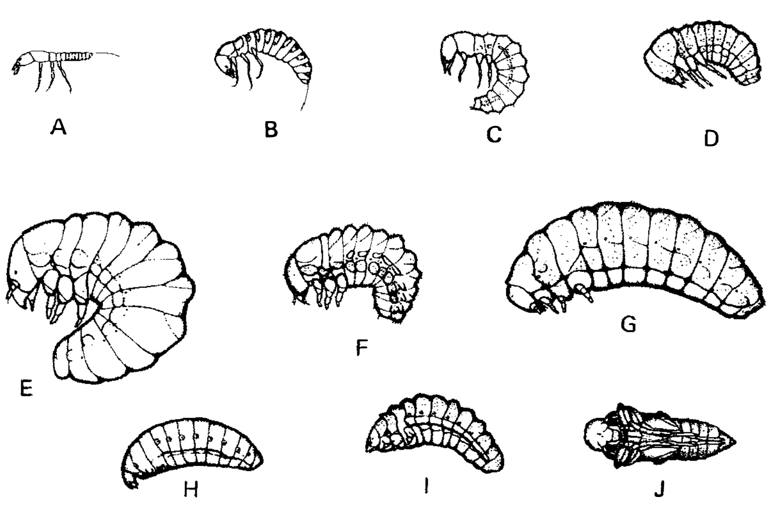

Figure 26–68 Larval and pupal instars of the black blister beetle, *Epicauta pennsylvanica* (De Geer), showing hypermetamorphosis. A, newly hatched first instar, or triungulin; **B**, fully fed first instar; **C**, second instar; **D**, third instar; E, fourth instar; F, newly molted fifth instar; G, gorged fifth instar; H, sixth instar (coarctate larva of pseudopupa); **I**, seventh instar; **J**, pupa. (Courtesy of Horsfall and the Arkansas Agricultural Experiment Station.)

Most blister beetles are elongate and somewhat cylindrical, but the species of *Cysteodemus*, which occur in the Southwest from Texas to southern California, have broadly oval and very convex elytra, and superficially resemble spiders (Figure 26–67D). These beetles are black, often with bluish or purplish highlights, and about 15 mm long.

***Family* Mycteridae—Palm and Flower Beetles:** Some members of this family (*Hemipeplus*, two species, found in Florida and Georgia) strongly resemble cucujids. They are elongate, slender, very flat, yellowish beetles, 8–12 mm long, with the front coxal cavities closed. These beetles are found under bark. Other mycterids (Mycterinae) have the front coxal cavities open, and some (for example, *Mycterus*, about 10 mm long) have the head extended anteriorly, much like the broad-nosed weevils. The body is more robust and not at all flattened. These beetles are generally found under rocks, in debris, or in vegetation. Both adults and larvae are said to be predaceous. The Mycterinae have been placed in the Salpingidae, but differ from them in having the penultimate tarsomere lobed. In the Salpingidae, this tarsomere is slender and similar to the other tarsomeres.

***Family* Boridae—Conifer Bark Beetles:** These beetles resemble tenebrionids, but have open fore coxal cavities and distinct lateral pronotal carinae They have been moved about in several families (e.g., Salpingidae, Pyrochroidae). Both larvae and adults live under bark. There are two genera, *Boros* and *Lecontia*, each with one species in the United States.

***Family* Pythidae—Dead Log Bark Beetles:** This family, which is best characterized by larval characters, is represented in North America by seven species in four genera; four of the species are in the genus *Pytho* (Figure 26–64C). Various researchers have placed these species in Pyrochroidae, Salpingidae, Boridae, and Mycteridae. Larvae feed under bark of both conifers and deciduous trees.

***Family* Pyrochroidae—Fire-Colored Beetles:** The pyrochroids are 6–20 mm long and are usually black, with the pronotum reddish or yellowish. About 50 species occur in North America, with 30 in the genus *Pedilus* (Figure 26–69B). The head and pronotum are narrower than the elytra, and the elytra are somewhat broader posteriorly. The antennae are serrate to pectinate (rarely filiform), and in some males almost plumose (Figure 26–66B), with long, slender processes on antennomeres 3–10. The eyes are often quite large. The short-lived adults are found on foliage and flowers and sometimes under bark. The larvae live under the bark of dead trees.

***Family* Salpingidae—Narrow-Waisted Bark Beetles:** This is an extremely variable group and difficult to characterize. Most of the 20 North American species of salpingids are black, elongate, and somewhat flattened. The adults and larvae are predaceous. The adults live under rocks and bark, in leaf litter, and on vegetation. The species of *Aegialites*, which occur along the Pacific Coast from California to Alaska, live in rock cracks below the high tidemark along the seacoast. These beetles are elongate-oval, 3–4 mm long, and black with a metallic luster. Five species of *Elacatis* (false tiger beetles) occur in the United States. They were formerly placed in a separate family and are now considered a subfamily (Othniinae) of Salpingidae.

***Family* Anthicidae—Antlike Flower Beetles:** These beetles are 2–12 mm long and somewhat antlike in appearance, with the head deflexed and strongly constricted behind the eyes, and with the pronotum oval. The pronotum in many species (*Notoxus*, Figure 26–69A, and *Mycinotarsus*) has an anterior hornlike process extending forward over the head. Anthicids generally live on flowers and foliage; some live under stones and logs and in debris; and a few live on sand dunes. There are around 230 species in North America.

***Family* Aderidae—Antlike Leaf Beetles:** The aderids (48 species in 11 genera in North America) are reddish

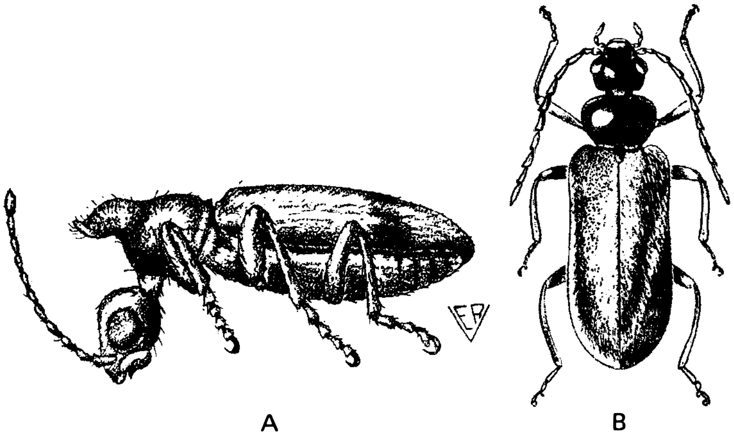

Figure 26–69 A, an antlike flower beetle, *Notoxus monodon* Fabricius (Anthicidae), 12×; B, a pyrochroid beetle, *Pedilus lugubris* Say, 5×. (Courtesy of Arnett.)

yellow to dark and 1.5 to 3.0 mm. long. They are very similar to the anthicids, but may be separated by the coarsely faceted, setose eyes and the head abruptly constricted at the base.

***Family* Scraptiidae—False Flower Beetles:** Most scraptiids may be recognized by their soft bodies, deeply emarginate eyes, and setose vestiture. They have been placed variously in Melandryidae, Mordellidae, and other families. Adults of some species are found on flowers, and others live under bark. In the North American fauna there are 46 species in 13 genera.

***Family* Polypriidae—The Red Cross Beetle:** A single species, *Polypria cruxrufa* Chevrolat, extends into south Texas. It is a moderate-sized beetle with strongly serrate antennae, deeply emarginate eyes, and brown elytra with a reddish cross-shaped mark. Nothing is known about the biology of this family, and the larva is unknown.

***Family* Cerambycidae—Long-Horned Beetles:** This family is a large one, with about 900 species in 300 genera occurring in the United States and Canada, and its members are all phytophagous. Most long-horns are elongate and cylindrical, with long antennae; the eyes are usually strongly notched or even completely divided; and many of these beetles are brightly colored. They vary from 3 to 60 mm long. The tarsi appear four-merous with the third tarsomere bilobed, but are actually five-merous. The fourth tarsomere is small and concealed in the notch of the third, and is often very difficult to see (Figure 26–10A). Both the Cerambycidae and Chrysomelidae have this type of tarsal structure, and these groups are sometimes difficult to separate. They can usually be separated by the characters given in the key (couplet 29).

Most adult cerambycids, particularly the brightly colored ones, feed on flowers. Many, usually not brightly colored, are nocturnal in habit and during the day may be found under bark or resting on trees or logs. Many ceramycids make a squeaking sound when picked up.

Most Cerambycidae are wood-boring in the larval stage, and many species are very destructive to shade, forest, and fruit trees and to freshly cut logs. The adults lay their eggs in crevices in the bark, and the larvae bore into the wood. The larval tunnels in the wood (Figure 26–70) are circular in cross section (unlike most buprestid tunnels, which are oval in cross section) and usually go straight in a short distance before turning. Different species attack different types of trees and shrubs. A few will attack living trees, but most species appear to prefer freshly cut logs or weakened and dying trees or branches. A few girdle twigs and lay their eggs just above the girdled band. Some bore into the stems of herbaceous plants. The larvae (Figure 26–71) are elongate, cylindrical, whitish, and almost legless and differ from the larvae of the Buprestidae in that the anterior end of the body is not broadened and flattened. They are often called "round-headed borers," to distinguish them from the flat-headed borers (larvae of Buprestidae).

This family is divided into eight subfamilies, which can generally be separated by the following key:


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Figure 26–70 Galleries of the poplar borer, *Saperda calcarata* Say.

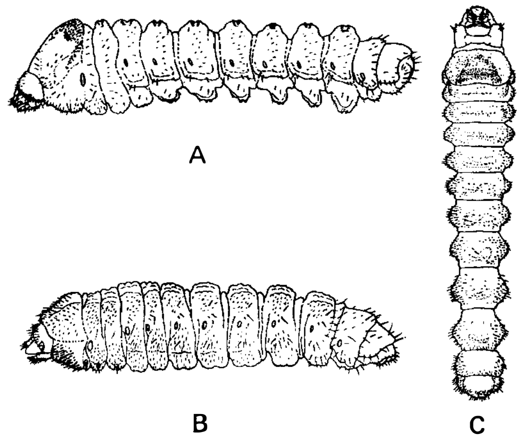


Figure 26–71 Cerambycid larvae. A, dogwood twig borer, *Oberea tripunctata* (Swederus), lateral view; **B**, twig pruner, *Elaphidionoides villosus* (Fabricius), lateral view; C, linden borer, *Saperda vestita* Say, dorsal view. (Courtesy of Peterson.)

Key to the Subfamilies of Cerambycidae

1.	Mandibles chisel-shaped (scalpriform); clypeus oblique to frons: wings lacking a spur on radiomedial crossvein (*Distenia*)	Disteniinae	p. 442
1′.	Mandibles not as in preceding entry, wings with a spur on the radiomedial crossvein	2	
2(1′).	Tarsi distinctly 5-5-5, without pubescent ventral pad; third tarsomere not dilated, concealing small fourth tarsomere (Figure 26–10J); antennae short, usually not attaining pronotal base	3	
2′.	Tarsi pseudotetramerous, with ventral pubescent pads; third tarsomere dilated, concealing true fourth tarsomere (Figure 26–10A); antennae long to very long, extending well beyond pronotal base	4	
3(2).	Pronotum with elevated lateral margins; labrum fused with epistoma	Parandrinae	p. 442
3′.	Pronotum without lateral margins; labrum free	Spondylidinae	p. 442
4(2′).	Head vertical or retracted; genal margin always directed posteriorly	Lamiinae	p. 444
4′.	Head obliquely inclined anteriorly or subvertical, genal margin never directed posteriorly	5	
5(4′).	Pronotum with elevated lateral margins; labrum fused with epistoma; fore coxae strongly transverse	Prioninae	p. 442
5′.	Pronotum without lateral margins; labrum free; fore coxae usually globular	6	
6(5′).	Stridulatory plate of mesonotum large (absent in a few), undivided	Cerambycinae	p. 445
6′.	Stridulatory plate of mesonotum divided by a median longitudinal stripe	7	
7(6′).	Head short, not narrowed behind eyes; second antennomere longer than broad, nearly half as long as third antennomere	Aseminae	p. 444
7′.	Head elongate, narrowed behind eyes; second antennomere not longer than broad, much less than half as long as third antennomere	Lepturinae	p. 445

Subfamily Disteniinae: *Distenia undata* (Fabricius) is the only representative of this subfamily in North America; it occurs in the eastern states. The mandibles are chisel-shaped and not serrate on the inner margin, and the thorax is spined on the sides and the elytra on the apex. It lives under bark of hickory and oak and on foliage of wild grape.

Subfamilies Parandrinae and Spondylidinae: These beetles differ from other cerambycids in having the fourth tarsomere plainly visible and the tarsi obviously five-merous (Figure 26–72E). The subfamily Parandrinae contains three species, two in the genus *Parandra*. These beetles are elongate-oval, somewhat flattened, bright reddish brown, and 9–18 mm long (Figure 26–73F). They look a little like small lucanids. They live under the bark of dead pine trees. The larvae burrow in dry, dead wood of logs and stumps.

The subfamily Spondylidinae contains two species, *Spondylis upiformis* Mannerheim, which occurs from the Great Lakes westward, and *Scaphinus muticus* (Fabricius), which occurs in the Southeast. These beetles are black, not particularly shiny, and 8–20 mm long. Their habits are similar to those of *Parandra*.

Subfamily Prioninae: This group contains the largest North American cerambycids, some of which may reach a length of about 75 mm. The Prioninae differ from the two preceding subfamilies in having the tarsi appearing four-merous and from the following subfamilies in having the pronotum margined laterally. Most have spines or teeth along the margins of the pronotum, and some have serrate antennae that contain 12 or more antennomeres. The most common species in this group belong to the genus *Prionus*. These beetles (Figure 26–74E) are broad and some-

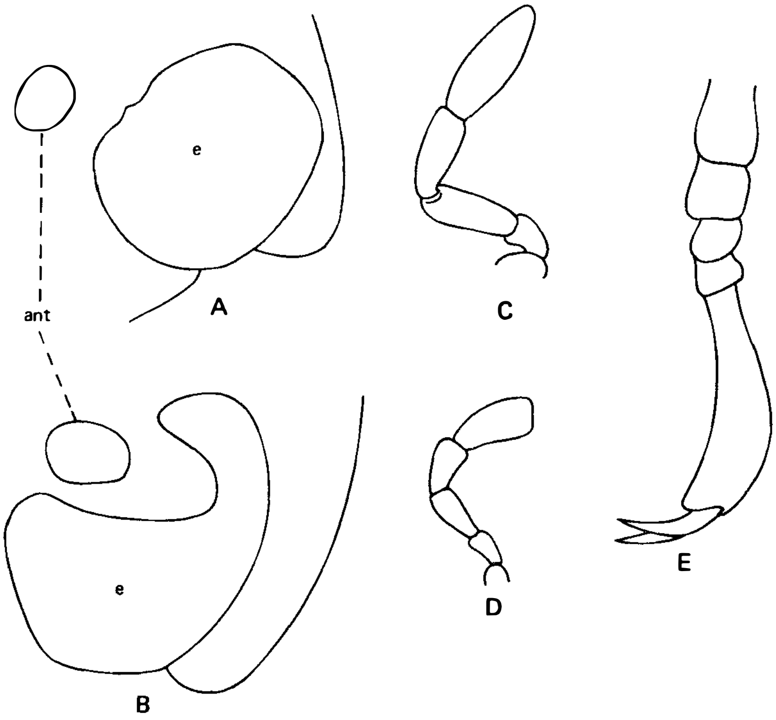


Figure 26–72 Characters of Cerambycidae. A and B, dorsolateral views of the left compound eye and the base of the antenna. A, base of antenna not surrounded by eye (*Toxotus*, Lepturinae); B, base of antenna partly surrounded by eye (*Elaphidion*, Cerambycinae); C and D, maxillary palps; C, *Monochamus* (Lamiinae); D, *Anoplodera* (Lepturinae); E, hind tarsus of *Parandra* (Parandrinae). *ant*, base of antenna; *e*, compound eye.

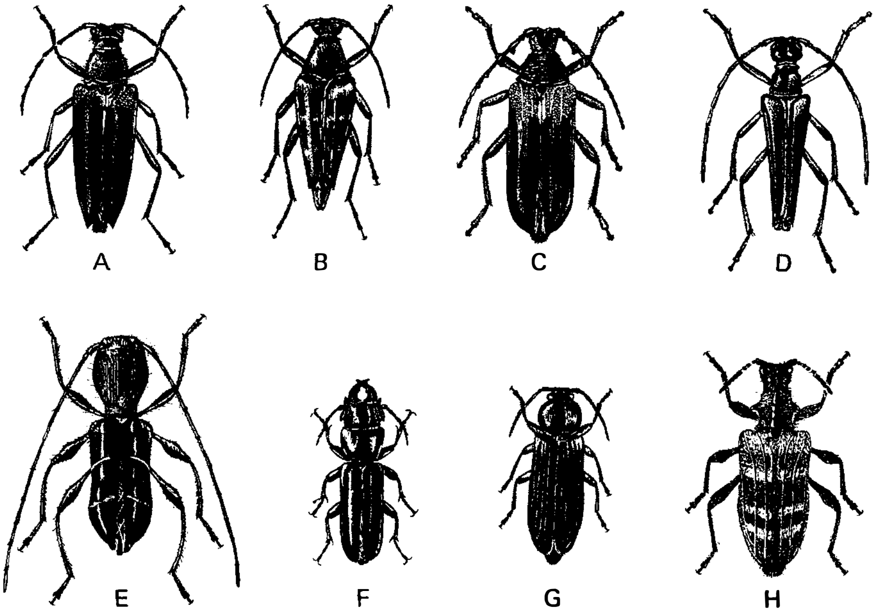


Figure 26–73 Long-horned beetles. A, *Anoplodera canadensis* (Olivier) (Lepturinae); B, *Typocerus deceptus* Knull (Lepturinae); C, *Desmocerus palliatus* (Forster) (Lepturinae); D, *Toxotus cylindricollis* (Say) (Lepturinae); E, *Euderces pini* (Olivier) (Cerambycinae); F, *Parandra polita* Say (Parandrinae); G, *Asemum striatum* (L.) (Aseminae); H, *Rhagium inquisitor* (L.) (Lepturinae). (Courtesy of Knull and the Ohio Biological Survey.)

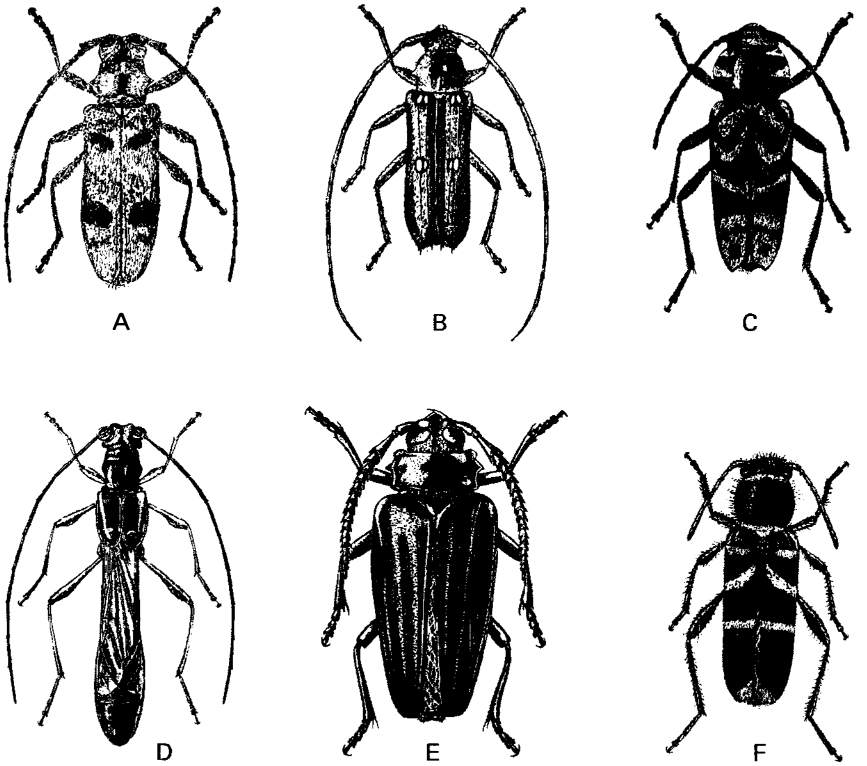
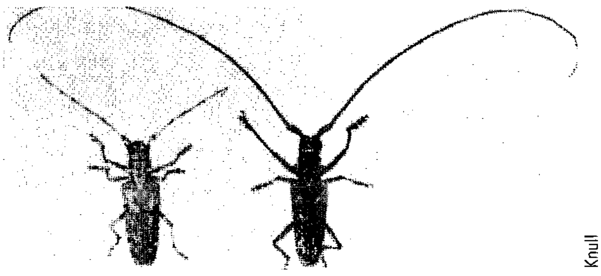


Figure 26–74 Long-horned beetles. A, *Goes tigrinus* (De Geer) (Lamiinae), 1½×; B, *Eburia quadrigeminata* (Say) (Cerambycinae), 1½×; C, the sugar maple borer, *Glycobius speciosus* (Say) (Cerambycinae) (natural size); D, *Necydalis mellita* (Say) (Lepturinae), 2×; E, *Prionus imbricornis* (L.) (Prioninae) (natural size); F, *Clytus marginicollis* Castelnau (Cerambycinae), 3×. (Courtesy of Knull and the Ohio Biological Survey.)



Knull

Figure 26–75 The northeastern sawyer beetle, *Monochamus notatus* (Drury), female at left, male at right. About ½×.

what flattened, blackish brown, with three broad teeth on the lateral margins of the pronotum, and 17–60 mm long (some western members of this genus are even larger). The antennae contain 12 or more antennomeres, and are serrate in the female. The members of the genus *Ergates*, which occur in the West, are also dark brown but have 8 or 10 small spines on each side of the pronotum, and the eyes are deeply emarginate. They are 35–65 mm long. *Orthosoma brunneum* (Forster), a fairly common eastern species, is long and narrow, light reddish brown, and 24–48 mm long. It has two or three teeth on the lateral margins of the pronotum.

Subfamily Aseminae: The members of this small group (22 species in six genera in North America) are elongate, parallel-sided, somewhat flattened beetles, usually black (sometimes with the elytra brownish), and mostly 10–20 mm long, with relatively short antennae (Figure 26–73G). Most have the eyes deeply emarginate (the eyes are completely divided in *Tetropium*) and partly surrounding the bases of the antennae. The larvae of these beetles principally attack dead pine trees and pine stumps.

Subfamily Lamiinae: The members of this subfamily can be recognized by the pointed terminal segment of the maxillary palps (Figure 26–72C) and the rather vertical face. They are elongated, parallel-sided, and usually somewhat cylindrical, with the pronotum often a little narrower than the base of the elytra (Figures 26–74A, 26–75). This group is a large one, and many species are of considerable economic importance.

The beetles in the genus *Monochamus* (Figure 26–75) are often called "sawyer beetles." They are usually over 25 mm long and are either black or a mottled gray. The first antennomere has a scarlike area near the tip. The antennae of the males are sometimes twice as long as the body. In the females the antennae are about as long as the body. The larvae feed on evergreens, usually on freshly cut logs, but they may sometimes attack living trees. The holes made by the larvae are at least as large in diameter as a lead pencil, and those of some species are nearly 13 mm in diameter.

The genus *Saperda* contains a number of important pest species. These beetles are about 25 mm long and are sometimes strikingly colored. *Saperda candida* Fabricius is white, with three broad, brown longitudinal stripes on the back. The larva bores in apple and other trees and is commonly called the "round-headed apple tree borer." Other important species in this genus are the poplar borer, *S. calcarata* Say, and the elm borer, *S. tridentata* Olivier.

The species in the genus *Oberea* are very slender and elongate. The raspberry cane borer, *O. bimaculata* (Olivier), is black, with the pronotum yellow and bearing two or three black spots. The larvae are often serious pests in canes of raspberries and blackberries.

The species of *Tetraopes* are about 13 mm long and are red with black spots. The compound eyes are divided so that there are apparently two compound eyes on each side of the head. The red milkweed beetle, *T. tetraophthalmus* (Forster) is a common species feeding on milkweed.

The twig girdler, *Oncideres cingulata* (Say), lays its eggs under the bark near the tips of living branches of hickory, elm, apple, and other deciduous trees. Before the egg is deposited, the beetle gnaws a deep groove around the twig, girdling it. The twig eventually dies and drops to the ground, and the larva completes its development in the twig.

The Asian long-horn beetle, *Anoplophora glabripennis* (Motschulsky), was recently introduced into the United States in wooden packing material. It threatens to become a major pest of hardwood trees, such as maple, elm, willow, and poplar.

Subfamily Lepturinae: The long-horns in this group resemble those in the Cerambycinae in having the terminal segment of the maxillary palps blunt or truncate at the apex (Figure 26–72D). They differ from the Cerambycinae in having the front coxae conical, and the bases of the antennae are usually not surrounded by the eyes (Figure 26–72A). Many Lepturinae have the elytra tapering posteriorly, or the pronotum narrower than the base of the elytra, giving them a rather broad-shouldered appearance.

A striking eastern species in this group is the elderberry long-horn, *Desmocerus palliatus* (Forster) (Figure 26–73C). This is a dark blue beetle about 25 mm long, with the basal third of the elytra orange-yellow, and with antennomeres 3–5 thickened at the tips. The adult lives on the flowers and foliage of elderberry, and the larva bores in the pith of this plant. Several other species of *Desmocerus* live on elderberry in the western states. They are similar in general coloration, with the males having brilliant scarlet elytra and a black pronotum. The females have very dark green elytra bordered narrowly with red along the outer margin.

This subfamily contains many species found on flowers. In most the elytra are broadest at the base and narrowed toward the apex (Figure 26–73A,B,D,H). Some common genera are *Stictopleptura*, *Typocerus*, *Toxotus*, and *Stenocorus*. Most of these beetles are brightly colored, often with yellow and black bands or stripes. In many cases the elytra do not cover the tip of the abdomen. All are excellent fliers.

Subfamily Cerambycinae: This group is a large one, and its members vary considerably in size and general appearance. One of the most strikingly marked species in this subfamily is the locust borer, *Megacyllene robiniae* (Forster), the larva of which bores into the trunks of black locust. The adult is black with bright yellow markings and is relatively common on goldenrod in late summer. Another easily recognized species in this group is *Eburia quadrigeminata* (Say), a brownish species 14–24 mm long, which has two pairs of elevated ivory-colored swellings on each elytron (Figure 26–74B). The members of some genera in this group (*Smodicum* and others) are somewhat flattened and have relatively short antennae. Others (for example, *Euderces*, Figure 26–73E) are small, shorter than 9 mm, and somewhat antlike in appearance.

***Family* Megalopodidae:** This small group, represented in the United States by nine species of *Zeugophora*, was formerly considered a subfamily of Chrysomelidae. The adults are 3–4 mm long and live chiefly on poplar, hickory, and oak.

***Family* Orsodacnidae:** This small family contains only four North American species in 3 genera. *Orsodacne atra* (Ahrens), a widely distributed beetle that is extremely variable in coloration, 7–8 mm long, is found chiefly on a wide variety of flowers, including those of willow and dogwood.

***Family* Chrysomelidae—Leaf Beetles:** The leaf beetles are closely related to the Cerambycidae, both groups having a similar tarsal structure (Figure 26–10A) and both being phytophagous. The leaf beetles usually have much shorter antennae and are smaller and more oval in shape than the cerambycids. The chrysomelids in the United States are almost all shorter than 12 mm; most cerambycids are larger. Many chrysomelids are brightly colored.

Adult leaf beetles feed principally on flowers and foliage. The larvae are phytophagous, but vary quite a bit in appearance and habits. Some larvae are free feeders on foliage, some are leaf miners, some feed on roots, some feed within seeds, and some bore in stems. Many members of this family are serious pests of cultivated plants. Most species overwinter as adults.

The family Chrysomelidae is a large one with approximately 1,720 North American species assigned to 195 genera. It is divided into a number of subfamilies, and those occurring in North America may be separated by the following key.

Key to the Subfamilies of Chrysomelidae

1.	Prothorax usually with well-defined lateral bead	2	
1′.	Prothorax usually without lateral bead	7	
2(1).	Head opisthognathous, front or vertex projecting strongly forward; tarsal formula 4-4-4	Hispinae	p. 450
2′.	Head usually prognathous or hypognathous, front or vertex not projecting strongly forward; tarsal formula 5-5-5, pseudotetramerous, with penultimate tarsomere minute and usually hidden between lobes of tarsomere 3	3	
3(2′).	Elytral epipleuron strongly angulate near basal third, excavate behind angulation for reception of apex of hind femur; pronotum with grooves at sides of prosternum for reception of antennae	Lamprosomatinae	p. 448
3′.	Elytral epipleuron not abruptly excavate near basal third (may be strongly curved); prosternal grooves for reception of antennae usually absent	4	
4(3′).	Abdomen with ventrites 2–4 usually greatly shortened medially; body subcylindrical, compact; head deeply inserted into prothorax; pygidium usually exposed, vertical	Cryptocephalinae	p. 448
4′.	Abdomen with intermediate ventrites not abnormally shortened; head usually not deeply inserted into prothorax body usually not subcylindrical	5	
5(4′).	Antennal insertions narrowly separated, usually by a distance less than length of basal antennomere	Galerucinae	p. 449
5′.	Antennal insertions widely separated, usually by distance much greater than length of basal antennomere	6	
6(5′).	Fore coxae transverse; ventral lobe of tarsomere 3 usually entire or weakly emarginate apically	Chrysomelinae	p. 448
6′.	Fore coxae globular; ventral lobe of tarsomere 3 deeply bilobed	Eumolpinae (in part)	p. 448
7(1′).	Eyes entire, not emarginate near antennal insertions	8	
7′.	Eyes emarginate near antennal insertions	9	
8(7).	Pretarsal claws bifid or appendiculate; head without deep median groove between antennae	Eumolpinae (in part)	p. 448
8′.	Pretarsal claws simple; head usually with deep median groove between antennae	Donaciinae	p. 447
9(7′).	Pygidium broadly exposed; hind femur greatly enlarged, often with large ventral teeth	Bruchinae	p. 447
9′.	Pygidium usually not exposed; hind femur not much larger than fore and mid femur	10	
10(9′).	Head with X-shaped groove between eyes; elytra usually not pubescent; pygidium not exposed	Criocerinae	p. 447
10′.	Head without X-shaped groove between eyes; elytra pubescent; pygidium exposed (but not broadly so)	Eumolpinae (in part)	p. 448

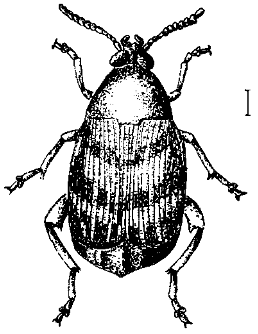


Figure 26–76 The bean weevil, *Acanthoscelides obtectus* (Say) (Chrysomelidae, Bruchinae). The line at the right represents the actual length. (Courtesy of USDA.)

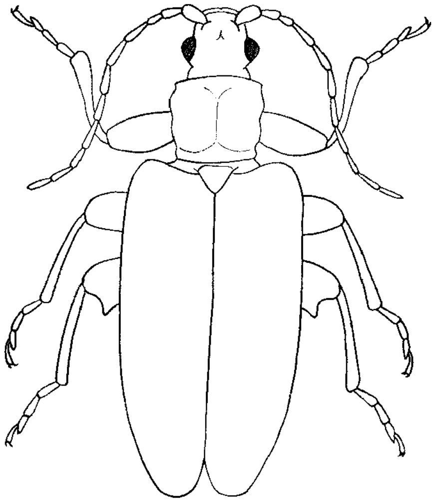


Figure 26–77 A long-horned leaf beetle, *Donacia* sp. (Chrysomelidae, Donaciinae), 7½×.

Subfamily Bruchinae—Seed Beetles: The members of this subfamily (134 species in North America) are short, stout-bodied beetles, mostly less than 5 mm long, with the elytra shortened and not covering the tip of the abdomen. The body is often somewhat narrowed anteriorly (Figure 26–76) and is usually dull grayish or brownish. The head is produced anteriorly into a short, broad snout.

The larvae of most bruchines feed inside seeds and pupate in the seeds. The adults generally oviposit on seeds that are fully developed or nearly so, but some oviposit on the flowers or young fruits. Some species develop in stored dry seeds. Some of the seed beetles, particularly those attacking leguminous plants, are serious pests. Two common species in this family are the bean weevil, *Acanthoscelides obtectus* (Say) (Figure 26–76), and the pea weevil, *Bruchus pisorum* (L.). These beetles lay their eggs on the pods of beans or peas, and the larvae bore into the seeds. The adults emerge through little round holes cut in the seed. The bean weevil may breed indoors throughout the year in stored dried beans, but the pea weevil attacks the peas only in the field and does not oviposit on dried peas. These insects cause serious damage in stored seeds that are not protected. The homemaker frequently sees bean weevils for the first time when the beetles try to escape through the windows, and can't figure out where they came from until later when he or she finds a sack of dried beans full of holes.

Subfamily Donaciinae—Long-Horned Leaf Beetles: These beetles are elongate and slender, and have long antennae (Figure 26–77). Most 56 North American species are dark-colored and metallic, 5.5 to 12.0 mm long, usually black, greenish, or coppery. They are active, fast-flying beetles and, in this respect, resemble the tiger beetles. The long-horned leaf beetles are seldom seen far from water. The adults are generally found on the flowers or foliage of water lilies, pondweed, sedges, and other aquatic plants. The eggs of many species are laid on the undersides of the leaves of water lily, in a whitish, crescent-shaped mass near a small, circular hole cut in the leaf by the adult. The larvae feed on the submerged parts of aquatic plants and obtain air through the plant stems. They pupate in cocoons that are fastened to vegetation below the water surface.

Subfamily Criocerinae: The members of this subfamily have the head narrowed behind the eyes to form a slender neck, and the punctures of the elytra are arranged in rows. Five genera occur in the United States: *Crioceris, Oulema, Neolema, Lilioceris,* and *Lema.* Some of these beetles are important pests.

The genus *Crioceris* includes two species, both imported from Europe, which attack asparagus and often cause serious damage. Both species are about 7 mm long. The striped asparagus beetle, *C. asparagi* (L.) has a red prothorax and light yellow markings on the bluish green elytra (Figure 26–78A). The spotted asparagus beetle, *C. duodecimpunctata* (L.), is orange, with six large black spots on each elytron. Adults and larvae of *C. asparagi* feed on the new shoots and cause damage to the growing plant. The larvae of *C. duodecimpunctata* feed inside the berries and do not injure the shoots.

The cereal leaf beetle, *Oulema melanopus* (L.) is blue-black with a red pronotum and about 6 mm long (Figures 26–78B, 26–79A). This serious introduced pest of grains has now spread throughout much of

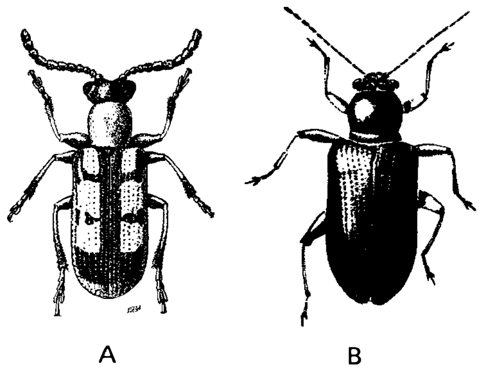


Figure 26–78 Criocerine leaf beetles. A, the striped asparagus beetle, *Crioceris asparagi* (L.); B, the cereal leaf beetle, *Oulema melanopus* (L.). (A, courtesy of the Utah State Agricultural College; B, courtesy of the Ohio Agricultural Research and Development Center.)

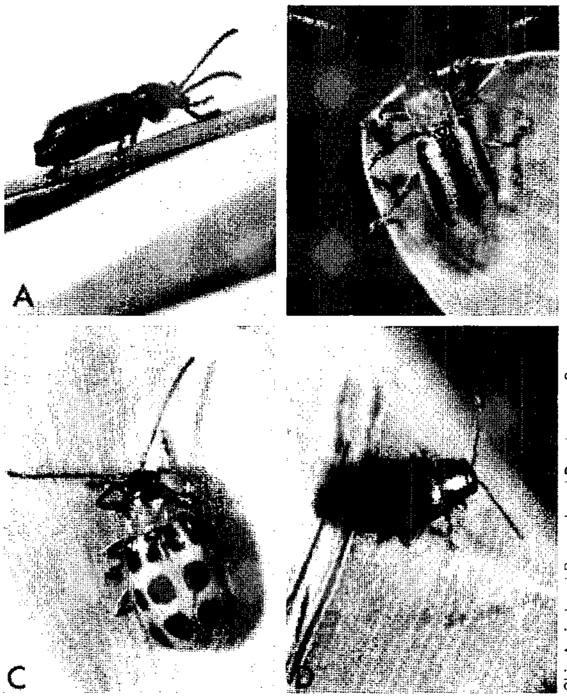


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Figure 26–79 Leaf beetles. A, the cereal leaf beetle, *Oulema melanopus* (L.) (Criocerinae); B, the striped cucumber beetle, *Acalymma vittatum* (Fabricius) (Galerucinae); C, the spotted cucumber beetle, *Diabrotica undecimpunctata howardi* Barber (Galerucinae); D, a flea beetle (Galerucinae).

North America. Both adults and larvae feed on the leaves of grain (and on various other grasses).

About 15 species of *Lema* occur in the eastern and southern United States. The most important species is probably the three-lined potato beetle, *L. trilinea* White, which feeds on potato and related plants. This beetle is 6–7 mm long and reddish yellow with three broad, black stripes on the elytra.

Subfamily Lamprosomatinae: This is one of the smallest chrysomelid subfamilies. Only one species, *Oomorphus floridanus* (Horn), occurs in the United States, in south Florida and the Keys.

Subfamily Cryptocephalinae (including Clytrinae and Chlamisinae)—Case-Bearing Leaf Beetles: The members of this large subfamily (more than 325 species in the United States), are small, robust, somewhat cylindrical beetles that have the head buried in the prothorax almost to the eyes. When disturbed, they draw in their legs, fall to the ground, and remain motionless. Many of these beetles are dark-colored, often with reddish or yellowish markings. The larvae are small fleshy grubs that crawl about dragging a small protective case, usually made of their own excrement. These cases are shorter than the body, and the posterior portion of the larva is bent downward and forward in the case. The larvae of most case-bearing leaf beetles feed on leaves or in leaf litter The larvae of some species live in ant nests, where they feed on vegetable debris. Pupation of these beetles occurs within the case.

Subfamily Eumolpinae (including Synetinae and Megascelidinae): This is one of the larger chrysomelid families, with about 145 species in 25 genera in North America. These are oblong, convex beetles that are often brown to black. Some are metallic in color or are yellowish and spotted. The dogbane beetle, *Chrysochus auratus* (Fabricius), which lives on dogbane and milkweed, is one of the most brilliantly colored of the leaf beetles. It is iridescent blue-green with a coppery tinge and is 8–11 mm long. A closely related species, *C. cobaltinus* LeConte, occurs in the West. It is darker and bluer than *C. auratus* and is 9–10 mm long.

The western grape rootworm, *Bromius obscurus* (L.), causes serious damage to grape crops, mostly in California, and also occurs in Europe and Siberia. Throughout most of its range in the United States from Alaska to New Mexico, its normal host is fireweed. Similar species found on grapes in the East belong to the genus *Fidia* and are small, oval, hairy, and dark brown to black.

Syneta albida LeConte, which damages the buds of many kinds of fruit trees along the North Pacific Coast, is a member of the Tribe Synetini.

Subfamily Chrysomelinae: Most members of this large subfamily 135 species in North America) are oval, convex, brightly colored, and 3.5 to 12.0 mm long, and

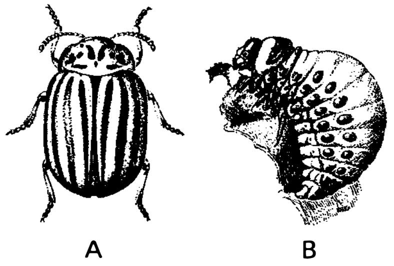

Figure 26–80 The Colorado potato beetle, *Leptinotarsa decemlineata* (Say). A, adult; B, larva. (Courtesy of the Utah Agricultural Experiment Station.)

the head is sunk into the prothorax almost to the eyes. The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), is the best-known and most important species in this group. This is a large, yellow beetle striped with black (Figure 26–80) and is a very serious pest of potato plants over most of the United States. Apparently the common name of this insect is inappropriate, because both the beetle and its native host plants, several species of nightshade (*Solanum*), originated in Mexico. The beetle did adapt to the cultivated potato and rapidly spread eastward, but from Nebraska, not Colorado. Since the introduction of the potato, this beetle has spread throughout the United States and has been transported to Europe, where it is also a serious pest. This group also includes the genus *Chrysolina*, species of which were introduced into the Unites States from Europe to control Klamath weed.

Most other species in this subfamily feed on various wild plants and are of little economic importance. Species of *Labidomera* (relatively large red and black beetles) feed on milkweed; *Phratora* (metallic blue or purple) feed on willow and poplar; and *Calligrapha* (whitish, with dark streaks and spots) feed on willow, alder, and other plants.

Subfamily Galerucinae (including Alticinae): The members of this group are small soft-bodied beetles, mostly 2.5 to 11.0 mm long, and many are yellowish with dark spots or stripes. The spotted cucumber beetle, *Diabrotica undecimpunctata howardi* Barber (Figure 26–79C), and the striped cucumber beetle, *Acalymma vittatum* (Fabricius) (Figure 26–79B), feed on cucumbers and related plants. These beetles do serious damage to cucurbits by their feeding, and they act as vectors of cucurbit wilt. The wilt bacilli pass the winter in the alimentary tract of the beetles, and new plants are inoculated when the beetles begin to feed on them in the spring. The larvae of these two species are small, white, and soft-bodied and feed on the roots and underground stems of cucurbits. The larva of the spotted cucumber beetle also feeds on the roots of corn and other plants and is sometimes called the "southern corn rootworm."

Two other corn rootworms—the northern corn rootworm, *Diabrotica barberi* Smith and Lawrence, and the western corn rootworm, *D. virgifera* LeConte—are serious pests of corn in the Midwest. Both adults and larvae cause damage, the larvae by feeding on the roots and the adults by feeding in the silk. The latter activity prevents pollination and consequent kernel development.

The elm leaf beetle, *Xanthogaleruca luteola* (Müller), is another important pest species in this group. It is a greenish yellow beetle with a few black spots on the head and pronotum and a black stripe down the outer margin of each elytron.

The flea beetles (Tribe Alticini) are small, jumping, leaf beetles that have the hind femora greatly enlarged. Many are metallic blue or greenish, but others are brown, black, or black with light markings (Figure 26–81). A number of the flea beetles are very important pests of garden and field crops. *Epitrix hirtipennis* (Melsheimer) attacks tobacco; *E. cucumeris* (Harris) feeds on potatoes and cucumbers; and *E. fuscula* Crotch feeds on eggplant and tomatoes. These are

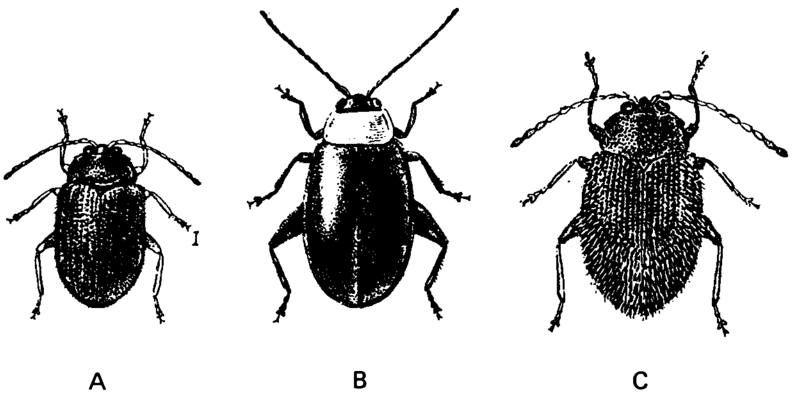

Figure 26–81 Flea beetles (Galerucinae, Alticini). A, the potato flea beetle, *Epitrix cucumeris* (Harris); B, the spinach flea beetle, *Disonychia xanthomelas* (Dalman); C, the eggplant flea beetle, *Epitrix fuscula* Crotch. (Courtesy of USDA.)

small brownish or blackish beetles about 2 mm long. *Altica chalybea* Illiger, a blue-black beetle 4–5 mm long, feeds on the buds and leaves of grape. Adult flea beetles feed on the leaves of the food plant and eat tiny holes in them. The leaves of a heavily infested plant look as if small shot had been fired into them. The larvae usually feed on the roots of the same plant.

The corn flea beetle, *Chaetocnema pulicaria* Melsheimer, is a vector of Stewart's disease of corn. The causative organism, a bacterium, overwinters in the alimentary tract of the adult beetle and is transmitted to seedling corn when the beetle feeds. This disease is especially important in early-planted sweet corn. In some instances entire fields have been destroyed by the disease.

Subfamily Hispinae—Leaf-Mining Leaf Beetles and Tortoise Beetles: The leaf-mining members of this subfamily (more than 100 species in the United States) are 4–7 mm long, elongate, and often peculiarly ridged (Figure 26–82). Most are leaf-mining in the larval stage, and some are rather serious pests. The locust leaf miner, *Odontota dorsalis* (Thunberg), an orange-yellow beetle with a broad, black stripe down the middle of the back (Figure 26–82), is a serious pest of black locust. Its mines are irregular blotches in the terminal half of the leaflet and, when numerous, may cause considerable defoliation.

Tortoise beetles are broadly oval or circular, with wide elytra and the head largely or entirely covered by the pronotum. Some are shaped very much like ladybird beetles. Many smaller tortoise beetles (5–6 mm long) are very brilliantly colored, often with golden color or markings; the mottled tortoise beetle, *Deloyala guttata* (Olivier), has black markings on a reddish gold background, and the golden tortoise beetle, *Charidotella sexpunctata bicolor* (Fabricius), is brilliant gold or bronzy, often with small black spots but without extensive black mottling. One of the largest members of this subfamily is the argus tortoise beetle, *Chelymorpha cassidea* (Fabricius), which is 9.5–11.5 mm long and shaped very much like a box turtle. It is red, usually with six black spots on each elytron and one black spot along the suture overlapping both elytra (Figure 26–83B).

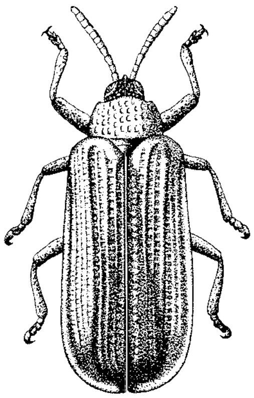

Figure 26–82 Adult of the locust leaf miner, *Odontota dorsalis* (Thunberg), 7× (Hispinae). (Courtesy of the Ohio Agricultural Research and Development Center.)

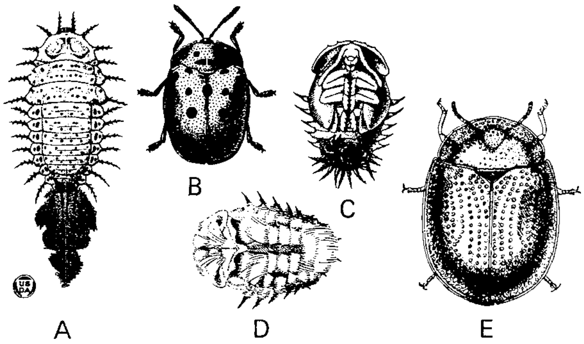

Figure 26–83 Tortoise beetles (Hispinae). A–D, the argus tortoise beetle, *Chelymorpha cassidea* (Fabricius), 1½×; E, the eggplant tortoise beetle, *Cassida pallidula* Boheman, 5×. A, larva, with the anal fork extended and covered with fecal material; B, adult; C, pupa, ventral view; D, pupa, dorsal view. (Courtesy of USDA.)

The larvae of tortoise beetles are elongate-oval and somewhat flattened. At the posterior end of the body is a forked process that is usually bent upward and forward over the body. Cast skins and excrement are attached to this process, forming a parasol-like shield over the body (Figure 26–83A). The larvae and adults of tortoise beetles feed principally on morning glories and related plants.

SUPERFAMILY Curculionoidea: The members of this group are sometimes called "snout beetles," as most have the head more or less prolonged anteriorly into a beak or snout. This term is less appropriate (and is seldom used) for the Platypodinae and Scolytinae, because the snout is scarcely developed in these two subfamilies of the Curculionidae. The Curculionoidea were formerly placed in a subdivision of the Coleoptera called the Rhynchophora.

Certain other characters besides the development of a snout distinguish the Curculionoidea from the beetles already described. The gular sutures are nearly always confluent, or lacking, with no gula developed (Figure 26–3C) (they are short but widely separated in the Nemonychidae). Prosternal sutures are lacking (except in the Anthribidae), and in most the palps are rigid or invisible and the labrum is absent (Figure 26–3A,B). The mouthparts are small and more or less hidden in most of these beetles. The mandibles, located at the tip of the snout, are usually the only mouthpart structures easily visible without dissection. The tarsi are five-merous, but usually appear four-merous (the fourth tarsomere is very small and hidden between the lobes of the third). The blind weevils of the subfamily Raymondionyminae of the Curculionidae have truly four-merous tarsi.

This is a large and important group of beetles, with more than 3,500 species occurring in North America. Practically all feed on plant materials, and most of the larvae are burrowing in habit, infesting nuts, twigs, and the like. The larvae are whitish, usually C-shaped, more or less cylindrical, and usually legless. A great many are of considerable economic importance as pests of field or garden crops, of forest, shade, and fruit trees, or of stored products. Recently, many species have been introduced into North America for the biological control of a variety of noxious or pest weeds.

Entomologists differ regarding the classification of the beetles in this superfamily. Lawrence and Newton (1995) group North American species into 7 families, but Alonso-Zarazaga and Lyal (1999) further subdivide these into 13 separate families. The more conservative classification recognizing only 7 families is followed here.

***Family* Nemonychidae—Pine Flower Snout Beetles:** This is a small group, with only five genera and 15 species occurring in North America. These beetles are 3.0 to 4.5 mm long, with the snout about as long as the prothorax and somewhat flattened and narrowed at the base. They differ from other families of Curculionoidea (except Anthribidae) in having the labrum distinct and the palps flexible. The larvae of these beetles develop in the staminate flowers of various conifers. Adults are usually found on conifers, but may occasionally be found on plum or peach trees. Kuschel (1989) provides a key to genera and species.

***Family* Anthribidae—Fungus Weevils:** The anthribids are elongate-oval, 0.5–30.0 (usually less than 10.0) mm long, with the beak short and broad and the antennae not elbowed (Figure 26–84B). Some species have slender antennae that may be longer than the body (hence they look a little like some Cerambycidae), and others have short antennae with a three-merous club. The elytra always cover the base of the pygidium, which is always partly exposed in lateral view but is usually not visible from above. The adults of this group are usually found on dead twigs or beneath loose bark. The larvae vary in habits. Some breed in woody fungi; some breed in the fungi of certain crops (for example, corn smut); some feed in seeds; and a few bore in dead wood. The introduced coffee bean weevil, *Araecerus fasciculatus* (DeGeer), is an important pest of seeds, berries, and dried fruits. There are approximately 90 described species of Anthribidae in the United States and Canada plus more than 30 that remain to be described.

***Family* Belidae—Primitive Weevils:** Only two species in this family occur in the United States, *Rhopalotria slossoni* (Schaeffer), and *R. mollis* (Sharp), both in southern Florida. The adults and larvae feed on the male cones of arrowroot (*Zamia*). Adults have non-geniculate (straight) antennae, the elytra are truncate (exposing the last one or two tergites), and the front legs are very robust in males. The role of these beetles in pollinating cycads has been studied by Norstog and Fawcett (1989).

***Family* Attelabidae—Leaf-Rolling Weevils, Tooth-Nosed Snout Beetles:** This family combines the traditional Attelabinae and Rhynchitinae despite their different structure and biology.

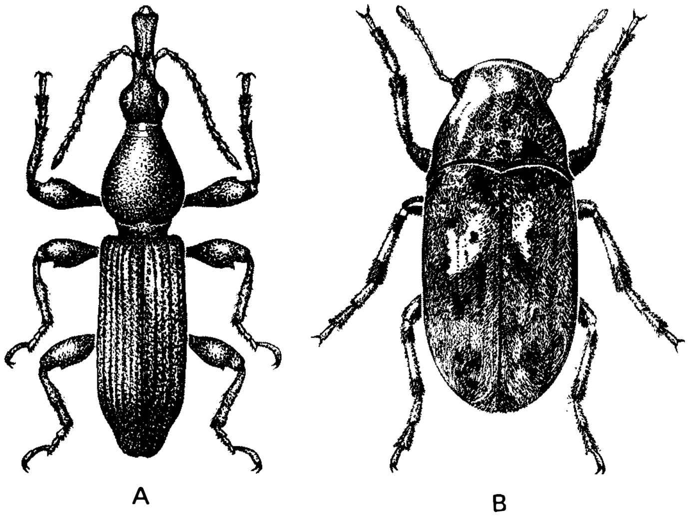

Figure 26–84 A, a straight-snouted weevil, *Arrhenodes minutus* (Drury) (Brentidae), 4×; B, a fungus weevil, *Euparius marmoreus* (Olivier) (Anthribidae), 6½×. (A, courtesy of Arnett; B, courtesy of Pierce and the U.S. National Museum.)

Attelabinae, the leaf-rolling weevils, are short and robust, 3–6 mm long. Most are black, reddish, or black with red markings. The most interesting characteristic of this group is their method of laying eggs, from which their common name is derived. When a female is ready to oviposit, she cuts two slits near the leaf base, from each edge to the midrib, and rolls the part of the leaf beyond these cuts into a neat, solid ball. A single egg is laid near the leaf tip, usually on the underside, before the leaf is rolled up. She then gnaws the midrib of the leaf (at the end of the basal cuts) partly in two, and the leaf roll eventually drops to the ground. The larva feeds on the inner portion of this leaf roll and pupates either in the roll or in the ground. There are five genera and 7 species of Attelabinae in North America. Most species live on oak, hickory, or walnut, but one species—*Attelabus nigripes* LeConte, red and 3.5 to 4.5 mm long)—feeds on sumac, and another—*Himatolabus pubescens* (Say), 4.5 to 5.5 mm long and dark reddish to black—feeds also on alder and hazelnut.

The thief weevil, *Pterocolus ovatus* (Fabricius), is a brood parasite of its relatives, the leaf-rolling weevils in the Attelabinae. Adults of this small, metallic-blue weevil enter leaf rolls of various attelabines, destroy the egg, and lay their own egg. The larvae then eats the leaf roll prepared by the host attelabine.

Rhynchitinae, the tooth-nosed weevils, are so named because they have teeth on the edges of the mandibles (Figure 26–85I). They are 1.5 to 6.5 mm long and usually live on low vegetation. There are

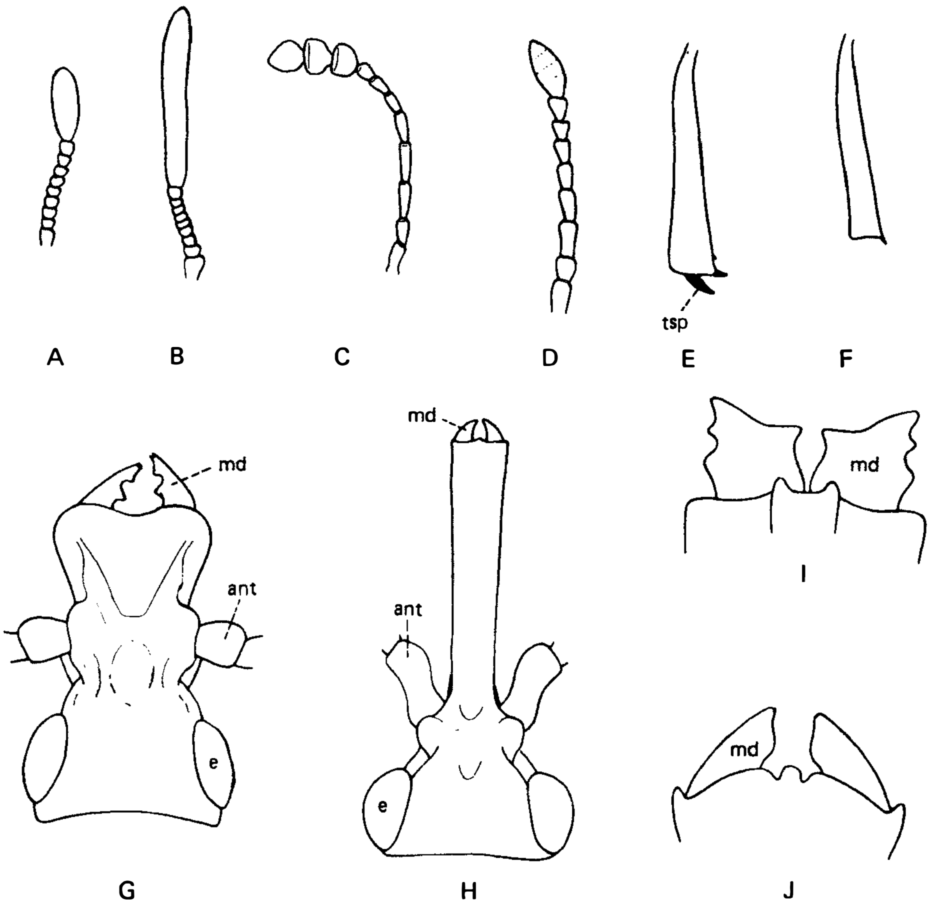

Figure 26–85 Characters of snout beetles. A–D, antennae; E–F, tibiae; G–H, heads; I–J, tip of snout. A, *Cylas*, female (Brentidae, Cyladinae); B, same, male; C, *Rhynchites* (Attelabidae, Rhynchitinae); D, *Ithycerus* (Ithyceridae); E, *Attelabus* (Attelabidae, Attelabinae); F, *Rhynchites* (Attelabidae, Rhynchitinae); G, *Arrhenodes*, male (Brentidae, Brentinae); H, same, female; I, *Rhynchites* (Attelabidae, Rhynchitinae); J, *Attelabus* (Attelabidae, Attelabinae). *ant*, antenna; *e*, compound eye; *md*, mandible; *tsp*, tibial spur.

about 45 North American species of these weevils, in eight genera. A common species in this group is the rose curculio, *Merhynchites bicolor* (Fabricius), which lives on roses. The adult is about 6 mm long and is red, with the snout and the ventral side of the body black, and it appears broad-shouldered. The larvae feed in rose fruits (hips). Other species in this group breed in buds, fruits, and nuts. Larvae of the species of *Eugnamptus* are dead leaf miners.

***Family* Brentidae—Straight-Snouted and Pear-Shaped Weevils:** Despite their remarkably different sizes and appearances, this family combines the traditional Brentinae, Apioninae (including Nanophyinae), and Cyladinae.

Brentinae are narrow, elongate, cylindrical beetles, 5.2 to 42.0 mm long, usually reddish or brownish and shining, with the snout projecting straight forward (Figure 26–84A). The snout is generally longer and more slender in the female than in the male (Figure 26–85G,H). This group is principally tropical, and only six species in 6 genera occur in North America. The only common eastern species is *Arrhenodes minutus* (Drury), which usually lives under the loose bark of dead oak, poplar, and beech trees. The larvae are woodboring and sometimes attack living trees.

Members of the Apioninae are small (4.5 mm long or less), somewhat pear-shaped, and usually blackish, and the antennae are usually not elbowed (excepting Nanophyinae in which antennae are elbowed). Most of the more than 150 North American species belong to the traditional genus *Apion*, many of which live on legumes and composites. The larvae bore into the seeds, stems, and other parts of the plant. Adults of the introduced hollyhock weevil, *A. longirostre* Olivier, feed on the leaves and buds of the hollyhock, and the larvae feed on the seeds of this plant. The pine gall weevil, *Podapion gallicola* Riley, forms galls on the twigs of pine trees. In recent years, some authors have subdivided the large traditional genus *Apion* into numerous smaller genera.

The sweet potato weevil, *Cylas formicarius elegantulus* (Summers), is an introduced species that lives principally in the southern states. This beetle is slender, elongate, antlike, and 5–6 mm long. The pronotum is reddish brown and the elytra are blue-black (Figure 26–86). The larvae are often called "sweet potato root borers." This insect is a serious pest of sweet potatoes because the larvae bore in the vines and roots, and the plants are often killed. The larvae may continue to burrow through the tubers after they are harvested, and adults may emerge after the sweet potatoes are in storage or on the market.

***Family* Ithyceridae:** This family includes a single species, the New York weevil, *Ithycerus noveboracensis* (Forster), which lives in eastern North America west to Nebraska and Texas. This beetle is shiny black, clothed with patches of gray and brown pubescence, and has the scutellum yellowish. It is 12–18 mm long. The adults of this beetle live principally on the limbs and foliage of hickory, oak, and beech trees. The larvae develop on the roots of these same trees.

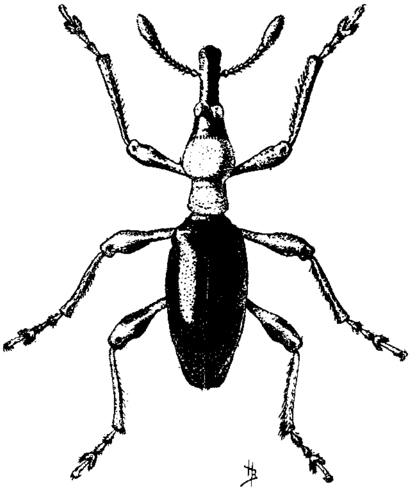

Figure 26–86 The sweetpotato weevil, *Cylas formicarius elegantulus* (Summers), female. (Courtesy of USDA.)

***Family* Curculionidae—Snout Beetles and True Weevils, including Bark and Ambrosia Beetles:** The members of this family are by far the most commonly encountered Curculionoidea. They may be found almost everywhere, and more than 3,000 species in almost 500 genera occur in North America. They show considerable variation in size, shape, and the form of the snout. The snout is fairly well developed in most species, with the antennae arising about the middle of the snout (Figure 26–3B). In some of the nut weevils (Figure 26–87C), the snout is long and slender, as long as the body or longer. Scolytinae, Platypodinae, and some Cossoninae lack a snout.

All members of this family (except a few occurring in ant nests) are plant feeders in both living and dead plants, and many are serious pests. Almost every part of a plant may be attacked, from the roots upward. The larvae usually feed inside the tissues of the plant, and the adults drill holes in fruits, nuts, and other plant parts.

Most snout beetles, when disturbed, will draw in their legs and antennae, fall to the ground, and remain motionless. Many are colored like bits of bark or dirt, and when they remain motionless they are very difficult to see. Some snout beetles (for example, *Conotrachelus*, subfamily Molytinae) can stridulate by rubbing hardened tubercles on the dorsum of the abdomen against filelike ridges on the underside of the elytra. These sounds in *Conotrachelus* (Figure 26–2) are ex-

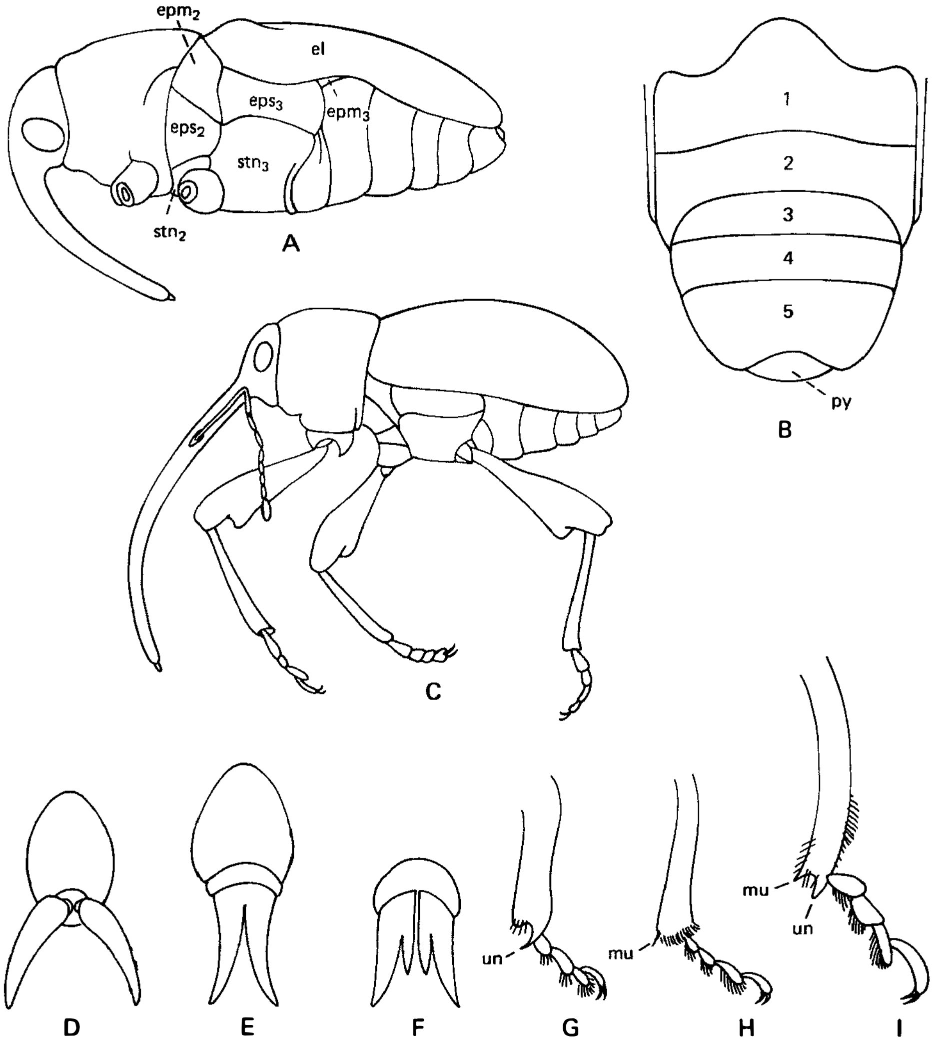

Figure 26–87 Characters of snout beetles. A, lateral view of body of *Odontocorynus* (Baridinae); B, ventral view of abdomen of *Tychius* (Curculioninae, Tychiini); C, a nut weevil, *Curculio* sp., lateral view (Curculioninae); **D–F**, tarsal claws; **D**, claws free and simple (*Ophriastes*, Entiminae); E, claws connate (*Cleonus*, Lixinae); F, claws toothed (*Rhyssematus*, Molytinae); G–I, tibia and tarsus; **G**, tibia uncinate (*Laemosaccus*, Mesoptiliinae); **H**, tibia mucronate (*Tychius*, Curculioninae, Tychiini); I, tibia mucronate and uncinate (*Erethistes*, Molytinae). *el*, elytron; *epm$_2$*, mesepimeron; *eps$_2$*, mesepisternus; *eps$_3$*, metepisternum; *mu*, mucro; *py*, pygidium; *stn$_2$*, mesosternum; *stn$_3$*, metasternum; *un*, uncus; *1–5*, ventrites 1–5.

tremely weak and usually can be heard only by holding the insect to one's ear.

Coleopterists differ regarding the limits of the family Curculionidae. We follow here the arrangement in *American Beetles*, in which the Curculionidae are divided into 18 subfamilies, including Scolytinae and Platypodinae, now generally regarded as closely related to snout beetles.

Key to the Subfamilies of Curculionidae

This key should serve to identify the vast majority of the specimens the general collector is likely to encounter. It is difficult to use in some places requiring high magnification and sometimes, dissections. There have been significant changes to the classification of Curculionidae since the last edition of this book. The key and classification used here follow the recent treatment of the family in the book *American Beetles* (Arnett et al. 2001, 2002), volume 2. Of most significance is the lower number of subfamilies. This is largely due to grouping of traditionally recognized subfamilies together within Curculioninae and Molytinae.

1.	Pregular sutures present; pregular sclerite distinct, located between median gular suture and labial articulation; head with rostrum virtually absent; at least 1 pair of tibiae with denticles or stout socketed setae along the dorsal (outer) margin	2	
1′.	Pregular sutures absent; pregular sclerite not evident; head with rostrum variable from very long and cylindrical to short and broad, or (rarely) nearly absent; tibiae lacking denticles or stout, socketed setae along the dorsal (outer) margin	3	
2(1).	Tarsus with tarsomere 1 as long as tarsomeres 2–5 combined; head as wide as pronotum; pronotum usually with lateral constriction near middle; antennal club without sutures; lateral denticles on front tibia not socketed	**Platypodinae**	p. 464
2′.	Tarsus with tarsomere 1 not longer than tarsomeres 2 or 3; head narrower than pronotum, often concealed by pronotum when viewed dorsally; pronotum not constricted laterally; antennal club with sutures; lateral denticles on front tibia socketed or (rarely) not	**Scolytinae**	p. 464
3(1′).	Tarsus of 4 subequal tarsomeres; eyes absent; body size small (<5 mm); body generally pale orange-red or pale brown; tibia at inner apical angle with small tooth much shorter than a pretarsal claw	**Raymondionyminae**	p. 459
3′.	Tarsus of 5 tarsomeres, but with tarsomere 4 very small and difficult to see between lobes of tarsomere 3; eyes absent or present, well developed, or reduced in size and represented by only from 1 to a few facets; body size variable; body color variable; tibia at apex variable, but if eyes are lacking or almost so, then tibia with large tooth arising from outer apical angle	4	
4(3′).	Tarsus with claws widely separated by dermal lobes extended between them from both dorsal and ventral surfaces at apex of tarsomere 5; mouthparts with prementum withdrawn into oral cavity, palpi mostly or entirely concealed; antenna inserted near base of rostrum, with scape long, projected some distance beyond the hind margin of the eye and not fitting into antennal scrobe (exceptions: *Dryophthorus*, *Orthognathus*, *Yuccaborus* have a more distal insertion of the antennae, possess a scrobe, and the scape does not pass, or only slightly passes, beyond hind margin of eye); antenna with club of 2 basic parts, with basal glabrous and shining portion, and apical uniformly pilose portion; funicle with 4, 5, or 6 antennomeres; body surface lacking broad, flat scales; pygydium formed of tergite 7 in male	**Dryophthorinae**[10]	p. 459

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[10] In small specimens it may be difficult to see the states of the pretarsal claws and the mouthparts. Only two small-sized genera of Dryophthorinae are included here. *Dryophthorus* can be recognized by an antennal funicle of four antennomeres in combination with the antennal club character, whereas *Sitophilus* may be recognized by the form of the apex of the hind tibia, which has a small preapical tooth on the inner margin in addition to the larger, hooklike tooth at the inner apical angle (the tibiae appearing "pincer-like"), in combination with the antennal club character.

4′.	Tarsus with claws single, connate at base or separate, but with dorsal and ventral surfaces at apex of tarsomere 5 not extended between bases of pretarsal claws; mouthparts with prementum visible, not withdrawn, palpi mostly visible; antenna inserted variously along length of rostrum, usually some distance from base, with scape short or long, and fitting into antennal scrobe, but at most only slightly projected beyond the hind margin of the eye; antenna with club various, but mostly with 3 antennomeres, each pilose to some extent, basal antennomere not or rarely shining, subequal in length to other antennomeres or rarely variously longer than other 2 antennomeres combined, sutures evident between all antennomeres; funicle with 5, 6, or 7 antennomeres; body surface mostly with some broad, flat scales or fine, hairlike scales; pygydium formed of tergite 8 in male	5		
5(4′).[11]	Male with aedeagus with tectum and pedon separate, tegmen as long as or longer than aedeagus (including the apodemes); species associated with freshwater aquatic habitats, many with dense, varnishlike coating over scales or with dense water-repellent scales		Erirrhinae	p. 459
5′.	Male with aedeagus with tectum and pedon fused, tegmen shorter than aedeagus (including the apodemes); species associated with various habitats, most with scales present, various in density, but lacking varnishlike coating (exception: *Bagous,* recognized by presence of prosternal channel) or with scales lacking entirely	6		
6(5′).[12]	Legs with well-developed, usually large hooklike tooth at apex of front, middle and hind tibiae: tooth arising from one of (a) outer apical angle, (b) from middle of apical margin, or (c) at inner apical angle, but if at inner apical angle, tooth on hind tibia more or less as long as or longer than pretarsal claw, and outer curved face of tooth is continuous with apex of outer tibial margin or connected to it by a distinct, continuous sharp carina that traverses the apical face of the tibia; apical comb of setae present or absent, if present, oriented either transversely, obliquely or subparallel to the length of the tibia	7		
6′.	Legs with apex of front, middle and hind tibiae with tooth, if present, small to moderately large (usually larger on front or middle tibiae), usually smaller than pretarsal claw, arising from inner apical angle and with outer curved face distinctly separated from, and not continuous with, outer tibial margin or with carina traversing the apical face of the tibia; apical comb of setae oriented transversely to length of tibia	18		
7(6).	Mesepimeron strongly ascended, truncated by elytral humeri and visible (or nearly so) in dorsal view between pronotum and elytra; tarsus with 1 (rarely) or 2 claws		Baridinae (major part)	p. 461
7′.	Mesepimeron not ascended, not visible in dorsal view between pronotum and elytra (exception; *Laemosaccus,* recognized by short, straight rostrum, basal margin of elytra extended over base of pronotum, exposed pygydium, and small, acute tooth on the inner margin of the front femur); tarsus with 2 claws	8		
8(7′).	Rostrum in repose received into ventral channel, which may be limited to prosternum or extended beyond into meso- or metasternum	9		

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[11] Unfortunately, dissection of a male is necessary to see the state of the primary character used here.

[12] This is often a difficult character to see clearly and to assess. Some groups (such as many Baridinae and some Curculioninae) are equivocal and are thus considered in both halves of this couplet. In general, taxa associated with woody plants tend to develop a larger and curved apical tooth, whereas those associated with herbaceous plants have a less developed tooth or apical spine, or none at all.

8′.	Rostrum in repose not received into ventral channel, but may rest between front, middle, or hind coxae	14	
9(8).	Eyes large, elongate-oval, subcontiguous (or nearly so) dorsally, frons very narrow; eyes situated toward top front of head, in lateral view with lower margin of eye clearly situated above level of dorsum of base of rostrum	Conoderinae	p. 462
9′.	Eyes small to moderate in size, more or less rounded, more widely separated dorsally, frons broad; eyes situated toward sides of head, in lateral view with lower margin of eye situated near or below level of dorsum of base of rostrum	10	
10(9′).	Rostrum very short, not much longer than wide, broad and flat dorsally, subquadrate in form; dorsal vestiture of pronotum and elytra in part bifid	Lixinae (part: *Bangasternus*)	p. 463
10′.	Rostrum moderately long, many times longer than wide, elongate and narrow; dorsal vestiture, if present, simple	11	
11(10′).	Ventral channel extended beyond prosternum into meso- or metasternum	Cryptorhynchinae	p. 462
11′.	Ventral channel limited to prosternum (even though rostrum in repose may overlie meso- or metasternum and some abdominal ventrites)	12	
12(11′).	Hind tibia with outer face at apex lacking apical comb of setae lateral to base of apical tooth; body with distinct and dense suberect or erect broad scales, body of some specimens with crustose coating	Cossoninae (part: Acamptini, *Acamptus*)	p.462
12′.	Hind tibia with outer face at apex with apical comb of setae lateral to base of apical tooth; body vestiture variable but surface not with crustose coating	13	
13(12′).	Body lacking distinct vestiture, with smooth, varnishlike coating over scales; elytra tuberculate or not; legs elongate, slender; commonly associated with aquatic habitats	Bagoinae	p. 461
13′.	Body with vestiture of appressed scales or suberect or erect hairlike scales, lacking smooth, varnishlike coating over scales, or obvious vestiture lacking; elytra tuberculate or not; legs more robust; rarely associated with aquatic habitats	Molytinae	p. 463
14(8′).	Mouthparts with labial palpi of 3 segments but short, globular, telescoping and appearing composed of 1 segment, ventrally situated at apex of large prementum; female with large, paired symbiont sacs attached to vagina near base of gonocoxites; body size mostly medium to large (>5 mm) (exception: *Microlarinus*)	Lixinae	p. 463
14′.	Mouthparts with labial palpi of 3 distinct segments but elongate, not telescoping, dorsally situated at apex of variably sized prementum; female lacking large, paired symbiont sacs attached to vagina near base of gonocoxites; body size mostly small to medium (<10 mm)	15	
15(14′).	One or more of mesepisternum, mesepimeron, metepisternum, and metepimeron with vestiture in form of dense plumose (pectinate) hairs, rarely hairs may be sparse, fine, and at most bifid only in anterior portion of metepisternum	16	
15′.	Mesepisternum, mesepimeron, metepisternum, and metepimeron with vestiture, if present, simple, not plumose or bifid	17	
16(15).	Tooth at apex of tibia, large and hooklike, larger than pretarsal claw; pronotum only slightly narrower than base of elytra in dorsal view; elytra with basal margin at intervals 2–4 extended anteriorly overlapping base of pronotum	Mesoptilinae	p. 463

16′.	Tooth at apex of tibia, small, at most subequal in length to pretarsal claw; pronotum distinctly narrower than base of elytra in dorsal view; elytra with basal margin at intervals 2–4 straight, not overlapping base of pronotum	Curculioninae (part: Otidocephalini)	p. 459
17(15′).	Hind tibia with outer face at apex with apical comb of setae lateral to base of apical tooth, oriented either transversely, obliquely, or subparallel to the length of the tibia	Molytinae (major part)	p. 463
17′.	Hind tibia with outer face at apex lacking apical comb of setae lateral to base of apical tooth	Cossoninae (major part)	p. 462
18(6′).	Mandible with prominent scar on outer apical face indicating point of attachment of deciduous process, or else clothed on outer apical face with many fine scales or setae, mandibles generally robust and thick; rostrum short and broad, usually quadrate or subquadrate in form, often expanded laterally toward apex, not different in males and females in length or form	Entiminae (major part)	p. 462
18′.	Mandible lacking scar and therefore lacking deciduous process, either glabrous or with a few small setae on outer apical face, mandibles generally less robust, smaller and thinner; rostrum more elongate and cylindrical, usually as long as or longer than pronotum, or (rarely) shorter than pronotum, sometimes different in males and females in length	19	
19(18′).	Rostrum in repose received into distinct ventral channel in prosternum (rarely into mesosternum)	20	
19′.	Rostrum in repose not received into ventral channel, but may rest between front, middle or hind coxae	23	
20(19).	Rostrum very broad, more or less triangular in dorsal view, fitting into large, deep emargination in front of front coxae; emargination limited posteriorly by small, triangular prosternum	Entiminae (part: Thecesternini, *Thecesternus*)	p. 462
20′.	Rostrum more elongate and cylindrical in form, prosternal channel extended behind front coxae (rarely onto mesosternum) and rostrum (when in repose) extended between or beyond front coxae	21	
21(20′).	Antenna with funicle with 5 antennomeres; prothorax lacking postocular lobes; claws free, simple; dorsum covered with fine, erect hairlike vestiture	Curculioninae (part: Mecinini, *Cleopomiarus*)	p. 459
21′.	Antenna with funicle with 6 or 7 antennomeres; other characters variable	22	
22(21′).	Pygydium covered by elytra; rostrum longer than pronotum, straight and slender, abruptly attenuate immediately beyond antennal insertion; antenna with antennomere 2 of funicle long, more or less one half length of scape	Baridinae (part: Madarini, Zygobaridina, *Amercedes*)	p. 461
22′.	Pygydium not covered by elytra; rostrum various in length, straight or slightly curved, more or less of uniform width throughout length, not abruptly attenuate; antenna with antennomere 2 of funicle short, much less than one half length of scape	Ceutorhynchinae (part)	p. 462
23(19′).	Mesepimeron strongly ascended, truncated by elytral humeri and visible in dorsal view between pronotum and elytra; pygydium not covered by elytra	Ceutorhynchinae (part)	p. 462
23′.	Mesepimeron not ascended, not visible in dorsal view between pronotum and elytra; pygydium mostly covered by elytra	24	
24(23′).	Tarsus with claws separate, each with basal process	Curculioninae (part)	p. 459
24′.	Tarsus with claws separate, simple	25	
25(24′).	Eyes rounded, rostrum mostly very elongate, slender and cylindrical in cross section; antenna with scape not or just reaching anterior margin of eye	Curculioninae (part)	p. 459

25′.	Eyes more or less elongate-oval, rostrum shorter, more robust and subquadrate in cross section; antenna with scape just reaching or passing anterior margin of eye	26	
26(25′).	Pronotum with anterolateral margin with distinct postocular lobe present	Cyclominae	p. 462
26′.	Pronotum with anterolateral margin straight, simple or postocular lobe at most very slightly developed	27	
27(26′).	Vestiture with at least some bifid scales (limited on some specimens to thoracic sterna), if bifid scales appear absent, humeri obviously quadrate; humeri quadrate to subquadrate, rarely rounded, if humeri rounded, bifid scales are distinct on dorsum	Hyperinae	p. 463
27′.	Vestiture simple, lacking bifid scales; humeri rounded	Entiminae (part)	p. 462

Subfamily **Dryophthorinae**—Billbugs and Grain Weevils: These beetles are stout-bodied and cylindrical and are of varying size. Some of the largest North American snout beetles belong to this group. The antennae arise close to the eyes, and the scape extends posterior to the eye (Figure 26–88E). The basal two thirds or more of the antennal club are smooth and shining. One of the largest billbugs is *Rhynchophorus cruentatus* (Fabricius), which is 20–30 mm long and lives on palms. The cocklebur weevil, *Rhodobaenus tredecimpunctatus* (Illiger), a common eastern billbug, is 7–11 mm long. It is reddish with small black spots on the elytra. The genus *Sphenophorus* (Figure 26–89) includes the corn billbugs, which live on various grasses, including timothy and corn. The adults feed on the foliage and the larvae bore into the stalks. Among the most important pests in this group are the granary weevil, *Sitophilus granarius* (L.), and the rice weevil, *S. oryzae* (L.). These are small, brownish beetles, 3–4 mm long, that attack stored grain (wheat, corn, rice, and so forth). Both adults and larvae feed on the grain, and the larvae develop inside the grains.

Subfamily **Erirrhininae:** This is a small but widely distributed group. The adults are usually found near water, as the larvae of many species develop in various aquatic plants. Many species are good swimmers.

Subfamily **Raymondionyminae:** This is a small group of only three genera of pale, eyeless weevils found in California and Oregon. The tarsi of these small weevils have only 4 tarsomeres. Adults are collected in leaf litter.

Subfamily **Curculioninae:** This subfamily is a large assemblage of taxa of questionable relationships. It includes the tribes Curculionini, Anthonomini, Gymnetrini, Otidocephalini, Rhamphini, and Tychiini.

The acorn and nut weevils of the genus *Curculio* are usually light brown and have a very long, slender snout that may be as long as the body or longer (Figure 26–87C). With their long snouts, the adults bore into acorns and other nuts and lay their eggs in some of these feeding holes. The larvae develop inside the nut. There are 27 species in North America; *C. nasicus* Say and *C. occidentis* (Casey) attack hazelnuts, and *C. caryae* (Horn), the pecan weevil, is a major pest of pecan.

Nearly 200 species of Anthonomini live in North America (more than 100 in the genus *Anthonomus*), and several are important pests of cultivated plants. The adults usually feed on fruits and lay their eggs in some of the feeding pits, and the larvae develop inside the fruits. The boll weevil, *A. grandis* Boheman, is a well-known and serious pest of cotton in the southern states. It entered the United States from Mexico in the late 1800s and has since spread over most cotton-growing sections of the country. The adults are about 6 mm long, reddish to brown, with a slender snout about half as long as the body. They feed on the fruit or bolls and flower buds and lay their eggs in the holes made in feeding. The larvae feed inside the buds and bolls and eventually destroy them. Other species of economic importance in this group are the strawberry weevil, *A. signatus* Say; the cranberry weevil, *A. musculus* Say; and the apple curculio, *A. quadrigibbus* Say. Some species are associated with mistletoes. Burke (1976) published a review of the biology of Anthonomini.

Flea weevils are so called because of their jumping habits. The hind femora are relatively stout. The larvae mine in the leaves of willow, elm, alder, cherry, and apple. The group is widely distributed and is represented in North America by 13 species in three genera: *Orchestes, Isochnus,* and *Tachyerges*.

The larvae of most Tychiini feed on the seeds of various legumes, and the adults live on the flowers. Four species of *Tychius*, including the clover seed weevil, *Tychius picirostris* (Fabricius), an important introduced pest of clover in the Northwest, are introduced into North America.

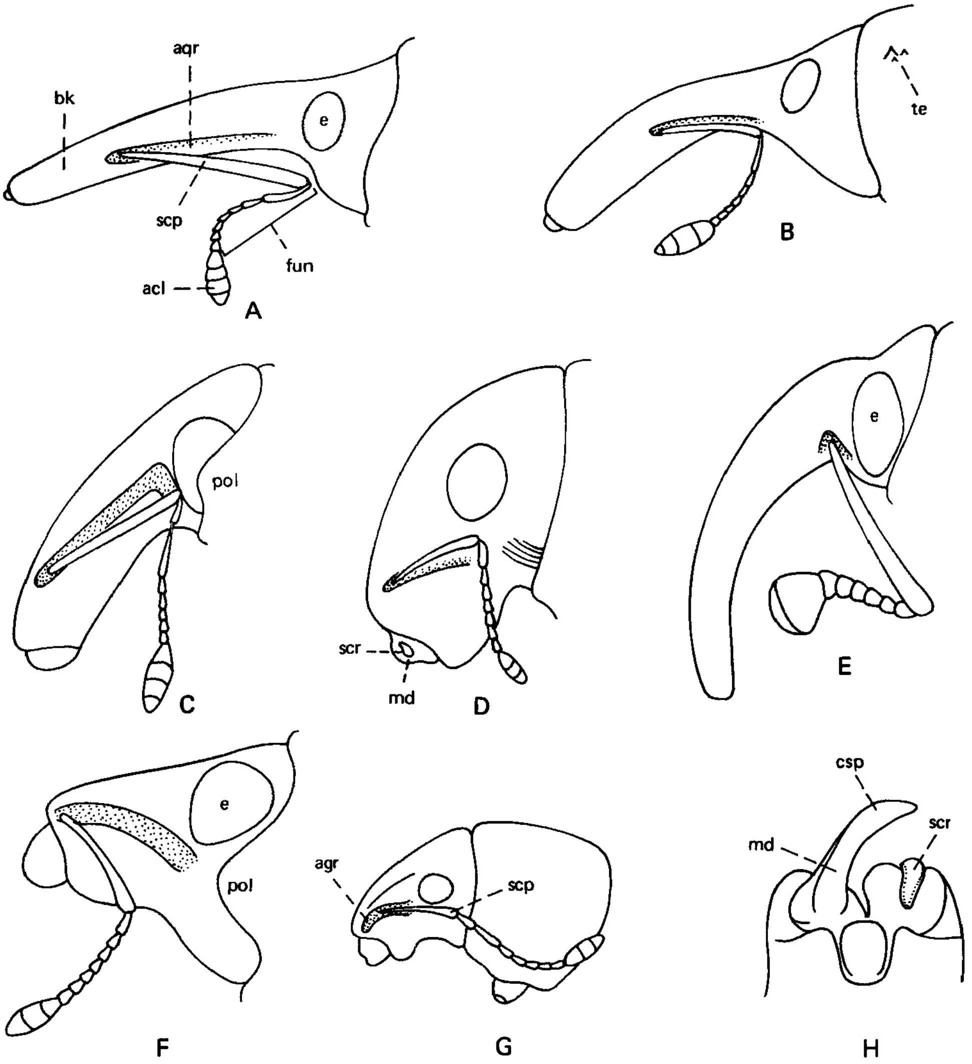


Figure 26–88 Characters of snout beetles. A–G, heads, lateral view; H, tip of snout, ventral view. A, *Anthonomus* (Curculioninae, Anthonomini); B, *Magdalis* (Mesoptiliinae); C, *Listronotus* (Cyclominae); D, *Pandeletelius* (Enteminae); E, *Rhodobaenus* (Dryophthorinae); F, *Eudiagogus* (Entiminae); G and H, *Pantomorus* (Entiminae). *acl*, antennal club; *agr*, scrobe; *bk*, beak of snout; *csp*, cusp of mandible; *e*, compound eye; *fun*, funiculus (antennal segments between scape and club); *md*, mandible; *pol*, postocular lobe of prothorax; *scp*, scape, the basal antennal segment; *scr*, scar left on mandible where cusp has broken off; *te*, teeth on prothorax.

The antlike weevils are small, shiny weevils whose prothorax is oval and narrowed at the base, and they thus resemble ants (Figure 26–90C). Some species develop in cynipid galls on oak, and some develop in twigs and stems. This group is a small one (in North America), and its members, most of which are in the genus *Myrmex*, are not very common.

Only seven species in the Mecinini occur in North America, but some of these are fairly common beetles. Some species develop in the seed pods of mullein (*Verbascum*), some develop in the seed pods of *Lobelia*, and another develops in galls at the base of plantain (*Plantago*). The six species in the genera *Gymnetron* and *Mecinus* are introduced.

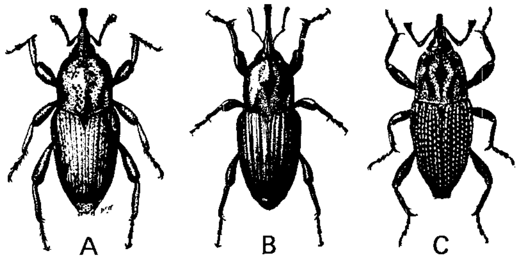


Figure 26–89 Billbugs (Dryophthorinae), 2×. A, the curlewbug, *Sphenophorus callosus* (Olivier); B, the maize billbug, *S. maidis* Chittenden; C, the timothy billbug, *S. zeae* (Walsh). (Courtesy of USDA.)

Subfamily Bagoinae: Two genera make up this subfamily in North America, all but one species in the genus *Bagous*. Adults are found in aquatic and semiaquatic habitats. They have a varnishlike coating on the body and are very similar in appearance to the aquatic Erirhininae.

Subfamily Baridinae: This is the largest subfamily of the Curculionidae, with about 500 North American species. These beetles are small and stout-bodied (Figure 26–90B) and can generally be recognized by the upward-extending mesepimera, which are sometimes visible from above (Figure 26–87A). Most species feed on various herbaceous plants; a few attack cultivated plants. The potato stalk borer, *Trichobaris trinotata* (Say), attacks potato, eggplant, and related plants. The

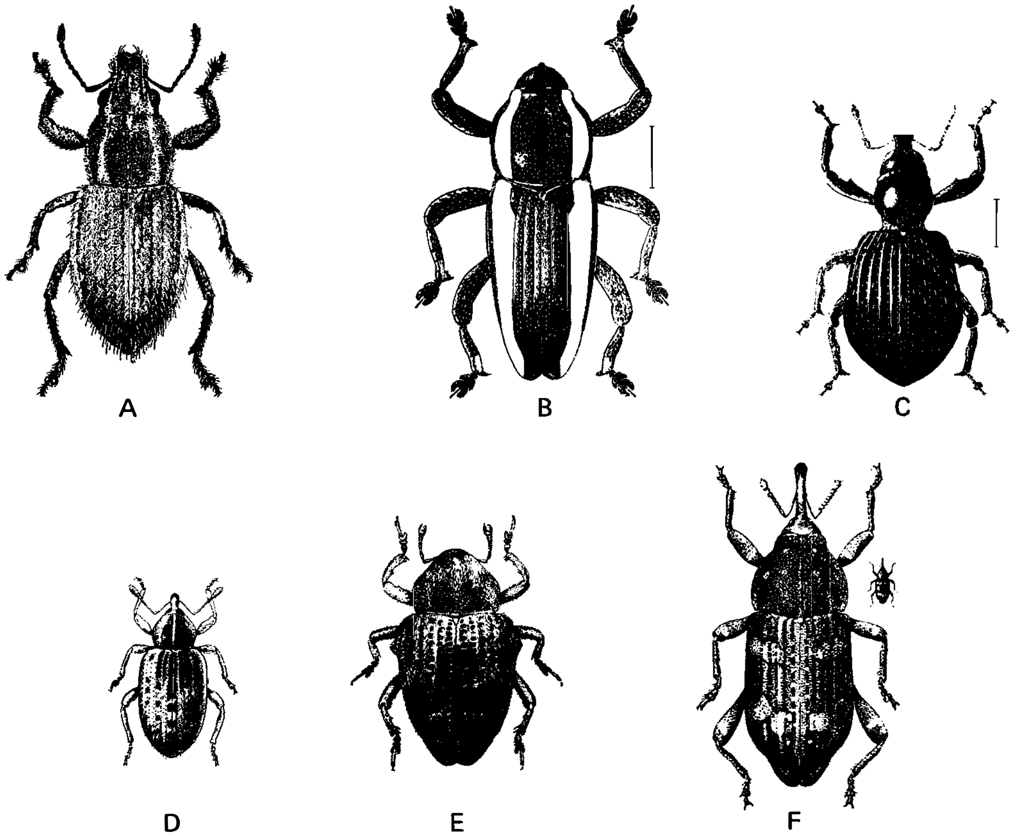


Figure 26–90 Snout beetles. A, a white-fringed beetle, *Naupactus leucoloma* (Boheman), 3½× (Entiminae); B, *Barinus bivittatus* (LeConte) (line = 1 mm) (Baridinae); C, an antlike weevil, *Myrmex subglaber* (Schaeffer) (line = 1 mm) (Curculioninae); D, the alfalfa weevil, *Hypera postica* (Gyllenhal) (Hyperinae), 5×; E, the bean stalk weevil, *Sternechus paludatus* (Casey) (Molytinae); F, the white pine weevil, *Pissodes strobi* (Peck) (insert is about one half natural size) (Molytinae). (A, D, E, and F, courtesy of USDA; B and C, courtesy of Sleeper.)

larvae bore in the stems, and the adults feed on the leaves. *Trichobaris mucorea* (LeConte) damages tobacco in the same way. The grape cane gallmaker, *Ampeloglypter sesostris* (LeConte), a stout-bodied reddish brown beetle, 3–4 mm long, makes galls on grape shoots. Much research needs to be done on this group of weevils.

Subfamily Ceutorhynchinae: This is a large and widely distributed group (over 150 North American species) and includes some important pests. The grape curculio, *Craponius inaequalis* (Say), a blackish, very broadly oval beetle about 3 mm long, feeds on grape foliage. The larvae develop in grape berries. The iris weevil, *Mononychus vulpeculus* (Fabricius), attacks iris. The larvae develop in the seed pods, and the adults feed in the flowers. Numerous species in the genus *Ceutorhynchus*, including the cabbage curculio, *Ceutorhynchus rapae* Gyllenhal, are pests of cultivated crucifers. A number of species of Ceutorhynchinae live in aquatic and semiaquatic habitats. Species in the genera *Phrydiuchus, Microplontus, Mogulones,* and *Trichosirocalus* have been deliberately introduced for biological control of pest weeds.

Subfamily Conoderinae: Formerly Zygopinae, this is a widely distributed group that is represented in North America by about 40 species. They feed on various herbaceous plants, mostly composites, and trees (including conifers); some are associated with *Agave* and some with mistletoes.

This subfamily includes the Tachygonini (toad weevils). These flattened, odd-looking weevils are usually found on the foliage of oak, elm, or locust. The larvae are leaf miners in these trees. Adults at rest usually hang downward from the leaves, hanging by means of their spiny hind femora. They frequently walk about on the underside of the leaves. This group is represented in the United States by five species of *Tachygonus*, which occur from the East to Arizona.

Subfamily Cossoninae—Broad-Nosed Bark Weevils: The Cossoninae can usually be recognized by the broad, short beak and the long, curved spine at the apex of each front tibia. These beetles are 1.5 to 6.5 mm long, and most are black and shiny. They live (often in great numbers) under the loose dead bark of trees and under logs. A few live under driftwood and along the seacoast. Some are associated with dead, fibrous leaves or stems of palms and *Agave*.

Subfamily Cryptorhynchinae: Many members of this group (187 North American species) have rough and tuberculate elytra. At rest the beak is usually drawn back into a deep groove in the prosternum, which also extends onto the front portion of the mesosternum. Adults are usually associated with dead wood, although some are found in living plants and some in seeds. Species of the genus *Tyloderma* are found in aquatic habitats. Many species are found in leaf litter, and the southwestern species *Liometophilus manni* Fall is associated with ants. Many species are flightless.

Subfamily Cyclominae: Most members of this group breed in aquatic or subaquatic plants, and the adults are found near water. A few are pests of vegetables. The vegetable weevil, *Listroderes costirostris obliquus* (Klug), attacks many different vegetables and is an important pest in the Gulf States and in California. In the large genus *Listronotus* (81 species), the carrot weevil, *L. oregonensis* (LeConte), is a pest of carrots and other vegetables in the East. *Emphyastes fucicola* Mannerheim is an odd-looking weevil that lives in decaying seaweed on sandy West Coast beaches.

Subfamily Entiminae—Broad-Nosed Weevils: The members of this subfamily (which includes the Otiorhynchini, Naupactini, Tanymecini, Thecesternini, and Tropiphorini) are commonly called the "broad-nosed weevils," because the snout is generally short and broad. Most are flightless, with the elytra fused together along the suture and the hind wings vestigial. This is a large and widely distributed group (with 124 genera in 24 tribes in North America) containing some important pests. Some important species in this group are the white-fringed beetles (three species of *Naupactus*), which are serious agricultural pests in the southern states. These beetles are about 12 mm long, with whitish elytral edges and with two longitudinal white stripes on the head and pronotum (Figure 26–90A). The white-fringed beetles are parthenogenetic; no males are known. Another injurious species in this group is the Fuller rose weevil, *Naupactus godmanni* (Crotch), 7–9 mm long. It attacks roses and many greenhouse plants, as well as citrus and other fruit trees. Like nearly all broad-nosed weevils, the larvae live in the soil and feed on the roots of the host plant, and the adults feed on the leaves. Members of the genus *Sitona* (mostly pale in color and 4–5 mm long) attack and seriously damage clovers. Members of the introduced species in the genus *Otiorhynchus* are very common and feed on a variety of plants. The strawberry root weevil, *O. ovatus* (L.), often causes serious injury to strawberries, and the black vine weevil, *O. sulcatus* (Fabricius), is an important pest of yew (*Taxus*). *Thecesternus affinis* LeConte, is a dull black beetle covered with brownish yellow scales and 6.5 to 9.0 mm long. At rest the head and beak are completely withdrawn into a large, triangular cavity in the front of the prothorax. These beetles live under stones or dried cow dung.

Many Entiminae are found in arid habitats, especially in the southwestern United States. Some have developed adaptations for sand dwelling that include dense, long hair over the body and broad legs adapted for digging. This group includes the weevils most often found at higher elevations.

Subfamily Hyperinae—Clover Weevils: Most members of this small group (17 North American species, all in the genus *Hypera*), feed on various clovers and are important clover pests. The alfalfa weevil, *H. postica* (Gyllenhal) (Figure 26–90D), and the clover leaf weevil, *H. punctata* (Fabricius), feed on the growing tips of the plant and skeletonize the leaves; *H. meles* (Fabricius) feeds in the clover heads. These beetles are dark-colored and 3–8 mm long.

Subfamily Lixinae: The most common beetles in this group are those in the genus *Lixus*, which are elongate and cylindrical, 10–15 mm long, with the curved beak nearly as long as the prothorax. They usually live on weeds near water. *Lixus concavus* Say, which breeds in the stems of dock, sunflower, and occasionally rhubarb, is commonly called the "rhubarb curculio." The adult is blackish, covered with gray pubescence. More than 100 species of Lixinae live in North America, 69 in the genus *Lixus*. Species in a number of genera have been introduced for biological control of pest weeds.

Subfamily Mesoptiliinae: These small, cylindrical weevils can usually be recognized by the toothlike processes on the anterior corners of the pronotum (Figure 26–88B, te). The larvae attack trees, usually tunneling in the twigs or under the bark. A few are pests of orchard or shade trees. Species of *Magdalis* (25 species in North America) are associated with various conifers and hardwoods.

Subfamily Molytinae: As with the Curculioninae, this group brings together a number of taxa previously placed in other subfamilies (for example, Hylobiini, Prionomerini, Cholini, Lepyrini, Lymantini, and Pissodini). Most notable is the reclassification of a number of weevils from the Cryptorhynchinae as Molytinae. This includes the large genus *Conotrachelus* and its relatives.

Most members of the Molytinae are dark-colored and of moderate size (Figure 26–91). Several species (especially species of *Hylobius*) are important pests of pine and other conifers. Species in the important genus *Pissodes* are usually brownish and cylindrical, most 8–10 mm long (Figure 26–90F); they are also important pests of conifers. The larvae tunnel in the terminal leader of a young tree and kill it, and one of the lateral branches becomes the terminal leader, giving rise to a tree with a bend partway up the trunk. Such a tree is of little value as a source of lumber. The white pine weevil, *Pissodes strobi* (Peck), is a common species attacking Eastern white pine.

One of the most important pest species in this group is the plum curculio, *Conotrachelus nenuphar* (Herbst) (Figure 26–92), which attacks plum, cherry, peach, apple, and other fruits. The females lay their eggs in little depressions they eat in the fruits and then cut a crescent-shaped incision beside the depression containing the egg. The larvae develop in the fruits and pupate in the soil. The adult is about 6 mm long, is dark-colored, and has two prominent tubercles on each elytron. The genus *Conotrachelus* is a large one (63 North American species), and its members are widely distributed. The larvae develop in various fruits and twigs. Larvae of species in the genera *Odontopus* and *Piazorhinus* are leaf miners in sassafras, tulip tree, and oak. The bean stalk weevil, *Sternechus paludatus* (Casey) (Figure 26–90E) is also a member of this subfamily.

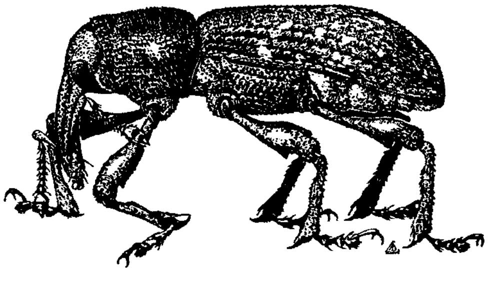


Figure 26–91 The pales weevil, *Hylobius pales* (Herbst) (Molytinae), 5× (Courtesy of USDA.)

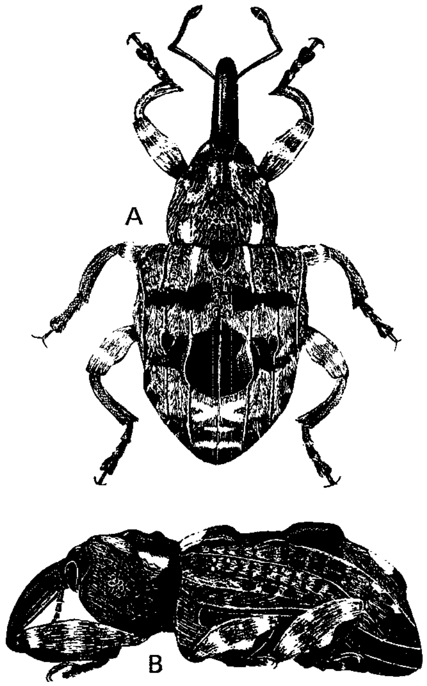


Figure 26–92 The plum curculio, *Conotrachelus nenuphar* (Herbst). A, dorsal view; B, lateral view of an individual feigning death. (Courtesy of Rings and the Ohio Agricultural Research and Development Center.)

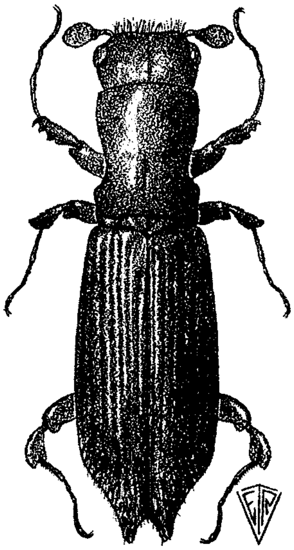


Figure 26–93 A pin-hole borer, *Platypus wilsoni* Swaine, 12× (Platypodinae). (Courtesy of Arnett.)

Subfamily Platypodinae—Pinhole Borers: The beetles in this group are elongate, slender, and cylindrical, with the head slightly wider than the pronotum (Figure 26–93). They are brownish and 2–8 mm long. The tarsi (which are 5-5-5) are very slender, with the first tarsomere longer than the remaining tarsomeres combined (Figure 26–10K). The antennae are short and geniculate and have a large, unsegmented club. The genus *Platypus* has recently been subdivided into four distinct genera. Only seven species occur in North America.

These beetles are wood-boring and bore in living trees, but seldom attack a healthy tree. They attack both deciduous trees and conifers. The larvae feed on fungi that are cultivated in their galleries.

Subfamily Scolytinae—Bark Beetles or Engravers, and Ambrosia Beetles: The scolytines are small, cylindrical beetles, rarely more than 6 or 8 mm long, and usually brownish or black (Figure 26–94). The antennae are short and geniculate and have a large, usually annulated club. The subfamily contains two groups: the bark beetles, which feed on the inner bark of trees, and the ambrosia beetles, which bore into the wood of trees and feed on an "ambrosial" form of a fungus, which they cultivate. Bark beetles differ from ambrosia beetles in having a large spine or projection at the apex of the front tibiae.

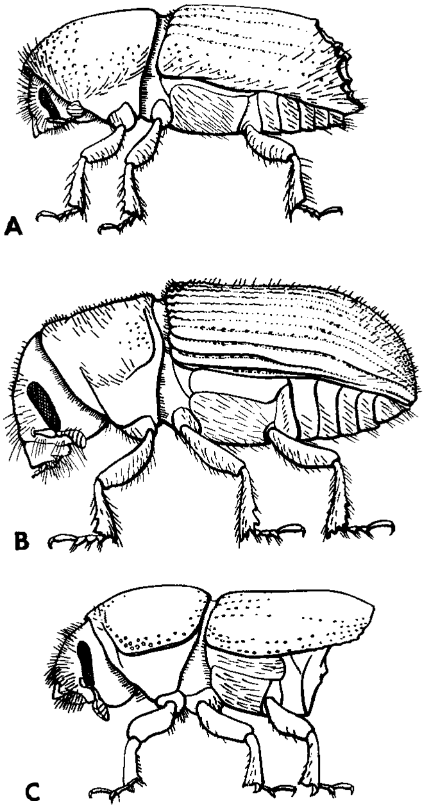


Figure 26–94 Bark beetles (Scolytinae). A, the pine engraver, *Ips pini* (Say); B, the Douglas fir beetle, *Dendroctonus pseudotsugae* Hopkins; C, the fir engraver, *Scolytus ventralis* (LeConte). (Courtesy of Rudinsky and Ryker, Oregon State Agricultural Experimental Station.)

The bark beetles live within the bark of trees, usually right at the surface of the wood, and feed on the succulent phloem tissue. Some species, especially in *Ips* and *Scolytus*, deeply score the sapwood and are often called "engravers." Although all bark beetles feed in dying trees, some species may infest living trees, especially conifers, and kill them. Most economically important scolytids are in three genera: *Dendroctonus, Ips*, and *Scolytus*. The infested tree is killed by the fungi (called "blue-stain" or "brown-stain") introduced by the adult beetles and spread by the larvae. As adults and larvae interrupt the flow of nutrients by feeding in the phloem, the fungus spreads inward and clogs the water transport vessels in the sapwood, suppressing the flow of lethal pitch into the beetle galleries. The destructive bark beetles exhibit a remarkable coordination of their flying population in a tightly synchronized mass attack, overwhelming the tree's defenses by sheer numbers. Both males and females respond to a combination of odors from the resin of the host tree and chemical signals (aggregation pheromones) from the first colonists. As a result, thousands of beetles may infest the same tree simultaneously.

In monogamous species such as *Dendroctonus pseudotsugae* Hopkins, the Douglas fir beetle, the female bores the gallery, releases pheromone, and accepts one male as her mate. In polygamous species such as *Ips pini* (Say), the pine engraver (Figure 26–94A), the male does the initial boring but constructs only a nuptial chamber in which to mate with the several females he accepts into his harem. Each female bores her own egg gallery out from the nuptial chamber.

As a female bark beetle constructs her egg gallery, the male cooperates with her by following along behind her, removing dust from the boring and shoving it out the entry hole. The female lays her eggs in little notches at intervals along the sides of the gallery. When the eggs hatch, the tiny, C-shaped, legless larvae begin eating their way through the phloem at right angles to the egg gallery. As the larvae grow and molt, moving farther away from the adult gallery, the frass-filled larval mines become larger, forming characteristic patterns (Figure 26–95). When the larvae complete their growth, they pupate at the ends of their mines. The adults emerge through round holes they bore through the bark. After a brood emerges, the surface of an infested tree appears peppered with shot holes.

Bark beetles have a greater impact economically on the timber-producing forests of North America than any other group of insects, being credited with the death of more than 4 billion board feet of sawtimber annually—over 90% of the total insect-caused mortality. Most tree mortality caused by bark beetles is caused by five species of *Dendroctonus*: the southern pine beetle, *D. frontalis* Zimmerman, in the South; the Douglas fir beetle, *D. pseudotsugae* (Figure 26–94B); the western pine beetle, *D. brevicomis* LeConte; the mountain pine beetle, *D. ponderosae* Hopkins; and the spruce beetle, *D. obesus* (Mannerheim), in the West. Infestations of bark beetles are recognized by fading foliage on groups of trees, by reddish brown frass or hardened pitch tubes on the trunk, or by evidence of large-scale woodpecker work on the bark. Patch killing of trees results from an aggregation of beetles flying to a source of attractant pheromone initially in one of the trees.

Each species of bark beetle has a characteristic pattern of adult and larval galleries and a rigid preference for a particular tree species. Many, if not all, scolytines transport tree fungi. Destructive species inoculate trees with blue- or brown-stain fungi, and ambrosia beetles depend on their fungi for food. The Dutch elm disease, transmitted by elm bark beetles, is caused by a fungus introduced from Europe with the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham). These beetles have spread the disease clear across the United States, from Boston to Portland, Oregon, in 75 years, completely eliminating American elms in many urban areas.

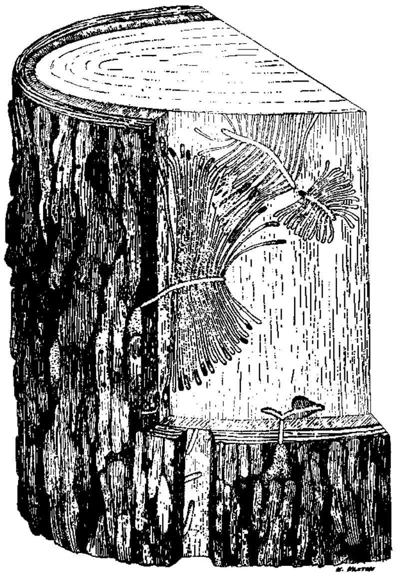


Figure 26–95 Semidiagrammatic drawing of a section of a log containing galleries of bark beetles (Scolytidae). The bark is cut through two entrance galleries, each with its accumulation of fine frass near the outside opening of the gallery. Three sets of galleries of different age are shown. In the one at the left the larvae are full grown and some have already pupated, and there is one empty pupal cell with its exit hole at the lower left corner of the cut-away section. Another entrance hole is evidenced by the frass accumulation on the bark at the left. (Courtesy of the Kaston and the Connecticut Agricultural Experiment Station.)

One agriculturally important species of bark beetle is the clover root borer, *Hylastinus obscurus* (Marsham), which often seriously damages clover. The larvae tunnel in the roots of clover, killing the plants.

Ambrosia beetles bore into the wood of trees, forming galleries in which both adults and larvae live. Only living or freshly killed trees, with a high moisture content, are infested. Although these beetles do not eat wood, the fungi they cultivate stain the wood, reducing its value. The presence of these beetles can cause entire shiploads of timber or lumber to be refused at a foreign port. The larvae of ambrosia beetles develop in small cells adjoining the main galleries, and in most species the adults feed the larvae. Each species usually feeds on one particular type of fungus. When the females emerge and fly to another tree, they carry conidia of the fungus from the natal tree to the new host and introduce the fungus into the gallery they excavate. After the eggs hatch, the females care for the larvae until they are full grown and pupate, keeping the larval niches supplied with fresh fungus or "ambrosia," and preventing the niche from being choked with frass or excess growth of fungus.

Collecting and Preserving Coleoptera

Because this is such a large and varied group, most methods discussed in Chapter 35 for collecting and preserving insects are applicable here. Several general collecting procedures, however, can be noted: (1) Many species can be taken by sweeping in a variety of situations; (2) many species, often strikingly colored, can be taken on flowers; (3) a number of species, such as the carrion beetles and others, can be obtained by means of suitably baited traps; (4) a number of species are attracted to lights at night and can be collected at lights or in a light trap; (5) beetles of many groups are to be found under bark, in rotting wood, under stones, and in similar situations; (6) many species can be obtained by sifting debris or leaf litter; and (7) many beetles are aquatic and can be collected by the various aquatic equipment and methods described in Chapter 35.

Most beetles are preserved pinned (through the right elytron) or on points. When mounting a beetle on a point, mount it so that the ventral side of the body and the legs are visible. The tip of the point can be bent down and the specimen attached to this bent-down tip by the right side of the thorax. It may sometimes be desirable to mount two specimens on the same point (when you are sure they are the same species), one dorsal side up and the other ventral side up. Many of the more minute beetles must be preserved in alcohol (70–80%) and mounted on a microscope slide for detailed study.

References

Alonso-Zarazaga, M. A., and C. H. C. Lyal. 1999. A world catalogue of families and genera of Curculionoidae (Insecta: Coleoptera): excluding Scolytidae and Platypodidae. Barcelona: Entomopraxis, 315 pp.

Arnett, R. H., Jr. 1967. Recent and future systematics of the Coleoptera in North America. Ann. Entomol. Soc. Amer. 60:162–170.

Arnett, R. H., Jr. 1968. The Beetles of the United States (a Manual for Identification). Ann Arbor, Mich.: American Entomological Institute, 1112 pp.

Arnett, R. H., Jr. (Ed.). 1978. Bibliography of Coleoptera of North America North of Mexico, 1758–1948. Gainesville, FL: Flora and Fauna Publications, 180 pp.

Arnett, R. H., Jr., and M. C. Thomas (Eds.). 2001. American Beetles, vol. 1. New York: CRC Press. 1443 pp.

Arnett, R. H., Jr., M. C. Thomas, P. E. Skelley, and J. H. Frank (Eds.). 2002. American Beetles, vol. 2. New York: CRC Press. 861 pp.

Arnol'di, L. V., V. V. Zherikhin, L. M. Nikritin, and A. G. Ponomarenko (Eds.). 1992. Mesozoic Coleoptera. Washington, DC: Smithsonian Institution Libraries.

Beutel, R. 1997. Über Phylogenese und Evolution der Coleoptera (Insecta), insbesondere der Adephaga. Abh. Naturwiss. Ver. Hamburg, 31:1–164.

Beutel, R., and F. Haas. 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). Cladistics 16:103–141.

Blatchley, W. S. 1910. An Illustrated and Descriptive Catalogue of the Coleoptera or Beetles (Exclusive of the Rhynchophora) Known to Occur in Indiana. Indianapolis: Nature, 1385 pp.

Blatchley, W. S., and C. W. Leng. 1916. Rhynchophora or Weevils of Northeastern North America. Indianapolis: Nature, 682 pp.

Bousquet, Y. (Ed.). 1991. Checklist of the Beetles of Canada and Alaska. Publ. 1861/E. Ottawa: Research Branch, Agriculture Canada, 430 pp.

Böving, A. G., and F. C. Craighead. 1931. An Illustrated Synopsis of the Principal Larval Forms of the Order Coleoptera. Entomol. Amer. (n.s.) 11(1–4):1–351.

Bradley, J. C. 1930. A Manual of the Genera of Beetles of America North of Mexico. Ithaca, NY: Daw, Illiston, 360 pp.

Bright, D. E., Jr. 1976. The Bark Beetles of Canada and Alaska. The Insects and Arachnids of Canada, Part 2. Ottawa: Canadian Government Publishing Centre, 241 pp.

Brown, D. J., and C. H. Scholtz. 1999. A phylogeny of the families of Scarabaeoidea (Coleoptera). Syst. Entomol. 24:51–84.

Brues, C. T., A. L. Melander, and F. M. Carpenter. 1954. Classification of insects. Bull. Mus. Comp. Zool. Bull., Harvard 73; 917 pp.

Burke, H. R. 1976. Bionomics of the anthonomine weevils. Annu. Rev. Entomol. 21:283–303.

Caterino, M. S., V. L. Shull, P. M. Hammond, and A. P. Vogler. 2002. Basal relationships of Coleoptera inferred from 18S rDNA sequences. Zoologica Scripta 31:41–49.

Cornell, J. F. 1972. Larvae of the families of Coleoptera: A bibliographic survey of recent papers and tabulary summary of seven selected English language contributions. Coleop. Bull. 26:81–96.

Craighead, F. C. 1950. Insect Enemies of Eastern Forests. U.S. Department of Agriculture, Misc. Publ. 657, 679 pp.

Crowson, R. A. 1960. The phylogeny of the Coleoptera. Annu. Rev. Entomol. 5:111–134.

Crowson, R. A. 1968. The Natural Classification of the Families of Coleoptera, 2nd ed. Oxford, UK: E. W. Classey, 195 pp.

Crowson, R. A. 1981. The Biology of the Coleoptera. London: Academic Press, 802 pp.

Dillon, E. S., and L. S. Dillon. 1961. A Manual of the Common Beetles of Eastern North America. Evanston, IL: Row, Peterson, 884 pp.

Downie, N. M., and R. H. Arnett, Jr. 1996. The Beetles of Northeastern North America, 2 vols. Gainesville, FL The Sandhill Crane Press, 1721 pp.

Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern (Eds.). 1979. Carabid Beetles: Their Evolution, Natural History, and Classification. The Hague: Junk, 644 pp.

Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. J. N.Y. Entomol. Soc. 93:1–912.

Gorham, J. R. (Ed.). 1991. Coleoptera. In Insects and Mite Pests in Foods: An Illustrated Key, pp. 75–227. Washington, D.C.: U.S. Department of Agriculture, Agriculture Research Service, U.S. Department Health and Human Service, 2 vols.

Hatch, M. H. 1953–1971. The Beetles of the Pacific Northwest. Part 1: Introduction and Adephaga. Seattle: University of Washington Press, 5 vols.

Headstrom, R. 1977. The Beetles of America. Cranbury, NJ: A. S. Barnes, 488 pp.

Hinton, H. E. 1945. A Monograph of the Beetles Associated with Stored Products London: British Museum, 443 pp.

Hlavac, T. F. 1972. The prothorax of Coleoptera: Origin, major features of variation. Psyche 79:123–149.

Hlavac, T. F. 1975. The prothorax of Coleoptera: (Except Bostrichiformia - Cucujiformia). Bull. Mus. Comp. Zool. 147:137–183.

Keen, F. P. 1952. Insect Enemies of Western Forests. U.S. Department of Agriculture. Misc. Publ. 273. 280 pp.

Kirejtshuk, A.G. 1992. Evolution of mode of life as the basis for division of the beetles into groups of high taxonomic rank. In M. Zunino, X. Bellés, and M. Blas (Eds.), Advances in Coleopterology, pp. 249–261. Barcelona: European Association of Coleopterology.

Kissinger, D. G. 1964. Curculionidae of America North of Mexico: A Key to the Genera. South Lancaster, MA: Taxonomic, 143 pp.

Klausnitzer, B. 1975. Probleme der Abgrenzung von Unterordnungen bei den Coleoptera. Entomologische Abhandlungen staatliches Museum für Tierkunde in Dresden 40:269–275.

Kukalová-Peck, J., and J. F. Lawrence. 1993. Evolution of the hind wing in Coleoptera. Can. Entomol. 125:181–258.

Kuschel, G. 1989. The Nearctic Nemonychidae (Coleoptera: Curculionoidae). Entomol. Scand. 20:121–171.

Larson, D. J., Y. Alarie, and R. E. Roughley. 2000. Predaceous Diving Beetles (Coleoptera: Dytiscidae) of the Nearctic Region, with Emphasis on the Fauna of Canada and Alaska. Monographs in Biodiversity. Ottawa: NRC Press, 982 pp.

Lawrence, J. F. 1982. Coleoptera. In S. Parker (Ed.), Synopsis and Classification of Living Organisms, pp. 482–553. New York: McGraw-Hill.

Lawrence, J. F. (coordinator). 1991. Order Coleoptera. In F. W. Stehr (Ed.), Immature Insects, vol. 2, pp. 144–658. Dubuque, IA: Kendall/Hunt, 975 pp.

Lawrence, J. E, and E. B. Britton. 1994. Australian Beetles. Carlton, Victoria: Melbourne University Press.

Lawrence, J. F., A. M. Hastings, M. J. Dallwitz, T. A. Paine, and E. J. Zurcher. 1999. Beetle Larvae of the World: Descriptions, Illustrations, and Information Retrieval for Families and Subfamilies. CD-ROM, Version 1.1 for MS-Windows. Melbourne: CSIRO Publishing.

Lawrence, J. E, A. M. Hastings, M. J. Dallwitz, T. A. Paine, and E. J. Zurcher. 1999. Beetles of the World: A Key and Information System for Families and Subfamilies. CD-ROM, Version 1.0 for MS-Windows. Melbourne: CSIRO Publishing.

Lawrence, J. F., and A. F. Newton, Jr. 1982. Evolution and classification of beetles. Ann. Rev. Ecol. Syst. 13:261–290.

Lawrence, J. E, and A. F. Newtond. 1995. Families and subfamilies of Coleoptera (with selected genera, notes and references, and data on family-group names). In Pakaluk, J., Slipinski, S. A. (Eds.), Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson, pp. 779–1006. Warsaw: Muzeum i Instytut Zoologii PAN. 2 vols.

Leech, H. B., and H. P. Chandler. 1956. Aquatic Coleoptera. In R. L. Usinger (Ed.), Aquatic Insects of California, pp. 293–371. Berkeley: University of California Press.

Leng, C. W., A. J. Mutchler, R. E. Blackwelder, and R. M. Blackwelder. 1920–1948. Catalogue of the Coleoptera of America North of Mexico. Mt. Vernon, NY: John D. Sherman. Original catalogue, 470 pp. (1920). First Supplement, by C. W. Leng and A. J. Mutchler, 78 pp. (1927). Second and Third Supplements, by C. W. Leng and A. J. Mutchler, 112 pp. (1933). Fourth Supplement, by R. E. Blackwelder, 146 pp. (1939). Fifth Supplement, by R. E. Blackwelder and R. M. Blackwelder, 87 pp. (1948).

Linsley, E. G. 1961–1964. The Cerambycidae of North America. Univ. Calif. Publ. Entomol. Part 1: Introduction; Univ. Calif. Publ. Entomol. 18:1–135 (1961). Part 2: Taxonomy and Classification of the Parandrinae, Prioninae, Spondylinae, and Aseminae; Univ. Calif. Publ. Entomol. 19:1–103 (1962). Part 3: Taxonomy and classification of the subfamily Cerambycinae, tribes Opsimini through Megaderini; Univ. Calif. Publ. Entomol. 20:1–188 (1962). Part 4: Taxonomy and classification of the subfamily Cerambycinae, tribes Elaphidionini through Rhinotragini; Univ. Calif. Publ. Entomol. 21:1–165 (1963). Part 5: Taxonomy and classification of the subfamily Cerambycinae, tribes Callichromini through Ancylocerini; Univ. Calif. Publ. Entomol. 22:1–197 (1964).

Linsley, E. G., and J. A. Chemsak. 1972–1976. Cerambycidae of North America. Part 6: Taxonomy and classification of the subfamily Lepturinae. Univ. Calif. Publ. Entomol. 69:1–138; illus. (1972); 80:1–186 (1976).

Moore, I., and E. F. Legner. 1979. An illustrated guide to the genera of Staphylinidae of America north of Mexico, exclusive of the Aleocharinae (Coleoptera). Berkeley: University of California, Division of Agriculture Science, 332 pp.

Norstog, K. J. and P. K. S. Fawcett. 1989. Insect-cycad simiosis and its relation to the pollination of *Zamia furfuracea* (Zamiaceae) by *Rhopalotria molli* (Curculionidae). Amer. J. Bot. 76:1380–1394.

O'Brien, C. W., and G. J. Wibmer. 1982. Annotated checklist of the weevils (Curculionidae *sensulato*) of North America, Central America, and the West Indies (Coleoptera: Curculionoidea). Mem. Amer. Entomol. Inst. 34, 382 pp.

Pakaluk, J., and S. A. Slipinski (Eds.). 1995. Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson. Warszawa [Warsaw]: Muzeum i Instytut Zoologii PAN.

Papp, C. S. 1983. Introduction to North American beetles. Sacramento, CA: Entomography Publications, 335 pp.

Peck, S. B., and M. C. Thomas. 1998. A distributional checklist of the beetles (Coleoptera) of Florida. Arthropods of Florida and Neighboring Land Areas 16:1–180.

Reichert, H. 1973. A critical study of the suborder Myxophaga, with a taxonomic revision of the Brazilian Torridinicolidae and Hydroscaphidae (Coleoptera). Arq. Zool. (São Paulo), 24(2):73–162

Rudinsky, J. A., P. T. Oester, and L. C. Ryker. 1978. Gallery initiation and male stridulation of the polygamous bark beetle *Polygraphus rufipennis*. Ann. Entomol. Soc. Amer. 71:317–321.

Rudinsky, J. A., and L. C. Ryker. 1976. Sound production in Scolytidae: Rivalry and premating stridulation of male Douglas fir beetle. J. Insect Physiol. 22:997–1003.

Ryker, L. C., and J. A. Rudinsky. 1976. Sound production in Scolytidae: Aggressive and mating behavior in the mountain pine beetle. Ann. Entomol. Soc. Amer. 69:677–680.

Ryker, L. C., and J. A. Rudinsky. 1976. Sound production in Scolytidae: Acoustic signals of male and female *Dendroctonus valens* LeConte. Z. Ang. Entomol. 80:113–118.

Van Tassell, E. R. 1965. An audiospectrographic study of stridulation as an isolating mechanism in the genus *Berosus* (Coleoptera: Hydrophilidae). Ann. Entomol. Soc. Amer. 58:407–413.

White, R. E. 1983. A Field Guide to the Beetles of North America. Boston: Houghton Mifflin, 368 pp.

Wood, S. L. 1979. Family Platypodidae. Catalogue of the Coleoptera of America North of Mexico, Fasc. 141, Washinton, D. C.: U.S. Department of Agriculture, Science, and Education Administration, 5 pp.

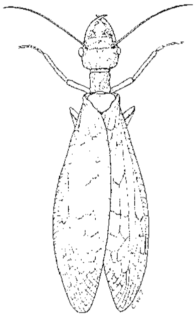
Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Gr. Basin Natur. Mem. 6, 1359 pp.

Wood, S. L. 1986. A reclassification of the genera of Scolytidae (Coleoptera). Gr. Basin Natur. Mem. 10, 126 pp.

27

Order Neuroptera[1,2]

Alderflies, Dobsonflies, Fishflies, Snakeflies, Lacewings, Antlions, and Owlflies



The Neuroptera are soft-bodied insects with four membranous wings that usually have a great many crossveins and extra branches of the longitudinal veins (hence the order name). There are generally a number of crossveins along the costal border of the wing, between the C and Sc. The radial sector often bears a number of parallel branches. The front and hind wings in North American species are similar in shape and venation and are usually held rooflike over the body at rest. The mouthparts are mandibulate, the antennae are generally long and have many segments, the tarsi have five segments, and cerci are absent.

These insects undergo complete metamorphosis. The larvae are generally campodeiform, with mandibulate mouthparts. Most larvae are predaceous, but those of the Sisyridae feed on freshwater sponges, and those of the Mantispidae are parasitic in the egg sacs of spiders. The mandibles of Megaloptera and Raphidioptera larvae are relatively short, while those of Planipennia larvae are long and sicklelike. In the Planipennia the feeding is done by sucking the body fluids of the victim through a narrow channel formed between the mandible and maxilla. In the Megaloptera and Raphidioptera, the pupae are naked, but in the Planipennia pupation occurs in a silken cocoon. The silk is produced by the Malpighian tubules and is spun from the anus.

Adult Neuroptera are found in a variety of situations, but those whose larvae are aquatic (Sialidae, Corydalidae, and Sisyridae) generally live near water. The adults are rather weak fliers. Most adults are predaceous. Some take only relatively weak prey, and adults of the Megaloptera probably feed little or not at all.

Classification of the Neuroptera

Some authorities divide the insects here included in the order Neuroptera, into three orders: Megaloptera, Raphidioptera, and Neuroptera. Others include the Raphidioptera in the Megaloptera. Entomologists generally accept that the three together form a monophyletic group, and thus the different classifications are consistent with the principles of phylogenetic systematics. We are treating these three groups as suborders.

An outline of the groups in the order, following that of Oswald and Penny (1991), is presented here. Alternative names or spellings are given in parentheses, and groups that are rare or unlikely to be taken by the general collector are marked with an asterisk (*).

Suborder Megaloptera (Sialodea)
    Sialidae—alderflies
    Corydalidae—dobsonflies and fishflies
Suborder Raphidioptera (Raphidiodea, Raphidioidea)—snakeflies
    Raphidiidae—raphidiid snakeflies
    Inocelliidae—inocelliid snakeflies, square-headed snakeflies
Suborder Planipennia (Neuroptera in the narrow sense)
    Superfamily Coniopterygoidea
        Coniopterygidae—dusty-wings*
    Superfamily Ithonoidea
        Ithonidae—ithonid lacewings*
    Superfamily Hemerobioidea
        Mantispidae—mantidflies
        Hemerobiidae (including Sympherobiidae)—brown lacewings

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[1] Neuroptera: *neuro*, nerve (referring to the wing veins); *ptera*, wings.

[2] Advice on this chapter was provided by Norman D. Penny.

Chrysopidae—common lacewings, green lacewings
Dilaridae—pleasing lacewings*
Berothidae—beaded lacewings*
Polystoechotidae—giant lacewings*
Sisyridae—spongillaflies
Superfamily Myrmeleontoidea
  Myrmeleontidae—antlions
  Ascalaphidae—owlflies

Two slightly different interpretations of wing venation are encountered in this order, that of Comstock and that of Carpenter and others. Most present workers, particularly those studying the Raphidioptera and Planipennia—following Martynov (1928), Carpenter (1936, 1940), and others—believe that an anterior branch of the media (labeled *MA* in our figures) persists in this order, branching from M near the base of the wing and usually fusing with Rs for a short distance. The differences in these two interpretations can be summarized as follows:

Comstock (1940)	Carpenter et al. (1940)
R_4	R_{4+5}
R_5	MA
Basal r-m	Base of MA
M	MP
M_{1+2}	MP_{1+2}
M_{3+4}	MP_{3+4}
Cu_1	CuA
Cu_2	CuP

We have followed Comstock's interpretation in labeling our figures of the Megaloptera and have followed the interpretation of Carpenter and others in labeling our figures of other wings in this order.

Key to the Families of Neuroptera

The families marked with an asterisk (*) in this key are relatively rare or are unlikely to be encountered by the general collector. Keys to larvae are given by Neunzig and Baker (1991) and Tauber (1991a, 1991b).

1.	Hind wings broader at base than front wings, with enlarged anal area that is folded fanwise at rest (Figure 27–1A,B); longitudinal veins usually forking near wing margin; larvae aquatic (suborder Megaloptera)	2	
1′.	Front and hind wings similar in size and shape, hind wings without enlarged anal area that is folded fanwise at rest (Figures 27–1C,D, 27–2, 27–3, 27–4)	3	
2(1).	Ocelli present; fourth tarsal segment cylindrical; body usually 25 mm or more long; wings hyaline or with smoky areas	Corydalidae	p. 475
2′.	Ocelli absent; fourth tarsal segment dilated and deeply bilobed; body usually less than 25 mm long; wings usually smoky (Figure 27–5)	Sialidae	p. 474
3(1′).	Wings with relatively few veins, Rs usually with only 2 branches (Figure 27–3A); wings covered with whitish powder; minute insects	Coniopterygidae*	p. 476
3′.	Wings with many veins, Rs usually with more than 2 branches (Figures 27–1C,D, 27–2, 27–3B,C, 27–4); wings not covered with whitish powder; size variable, but usually not minute	4	
4(3′).	Prothorax elongate (Figure 27–8)	5	
4′.	Prothorax of normal size, not elongate	7	
5(4).	Front legs raptorial, arising from anterior end of prothorax (Figure 27–8B); mantid-like insects, widely distributed	Mantispidae	p. 477
5′.	Front legs not raptorial, arising from posterior end of prothorax (Figure 27–8A); western United States (suborder Raphidioptera)	6	
6(5′).	Ocelli present; stigma in front wing with a crossvein; hind wings with Cu_2 and 1A fused for short distance, basal m-cu transverse (Figure 27–1C)	Raphidiidae	p. 476
6′.	Ocelli absent; stigma in front wing without crossvein; hind wings with Cu_2 and 1A separate, basal m-cu oblique (Figure 27–1D)	Inocelliidae	p. 476

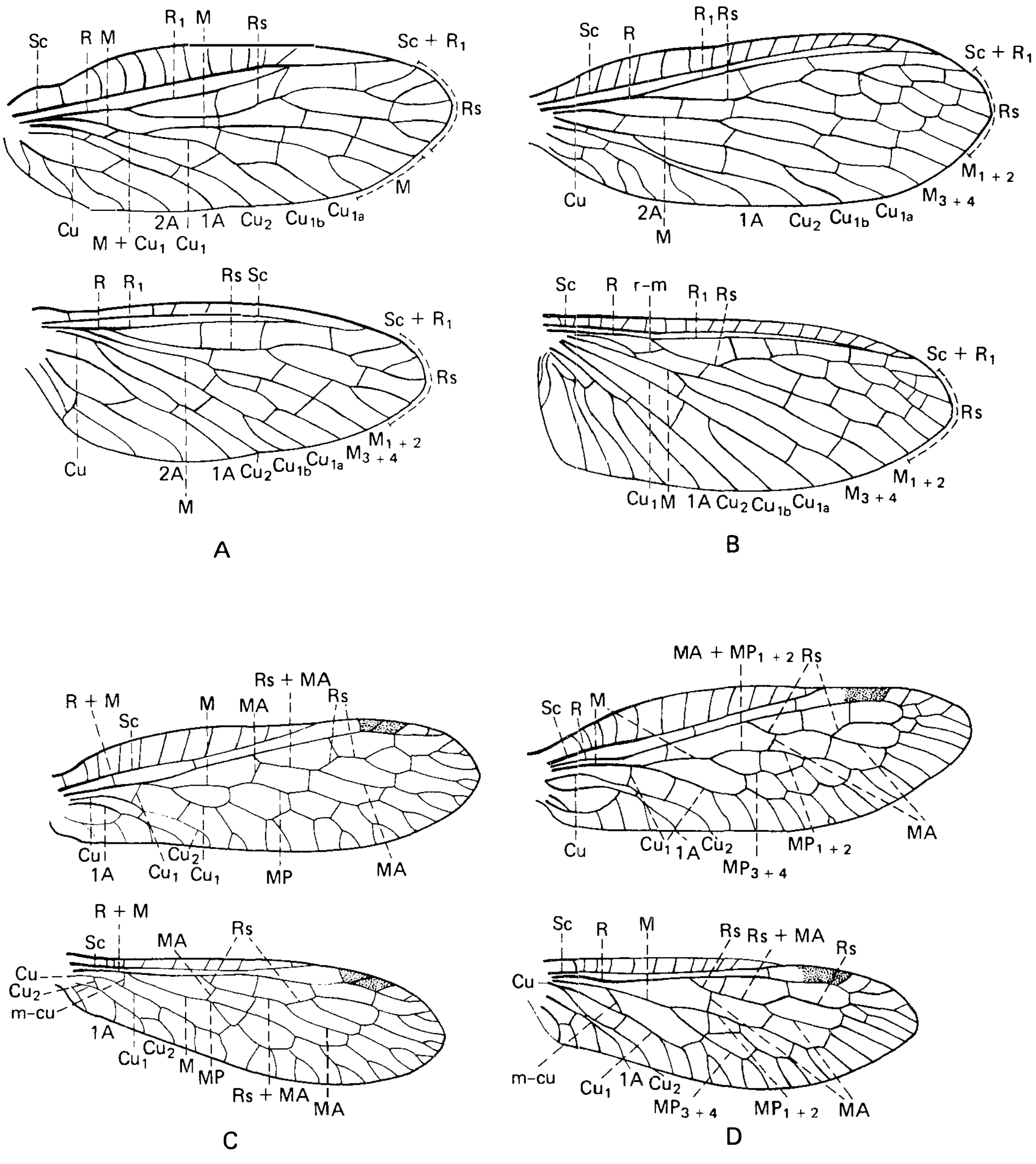


Figure 27–1 Wings of Neuroptera. A, *Sialis* (Sialidae); **B**, *Nigronia* (Corydalidae); C, *Agulla* (Raphidiidae); **D**, *Negha* (Inocelliidae). The venation in A and B is labeled with the interpretation of Comstock (1940), and in C and D with the interpretation of Carpenter (1936) and others. MA, anterior media; MP, posterior media.

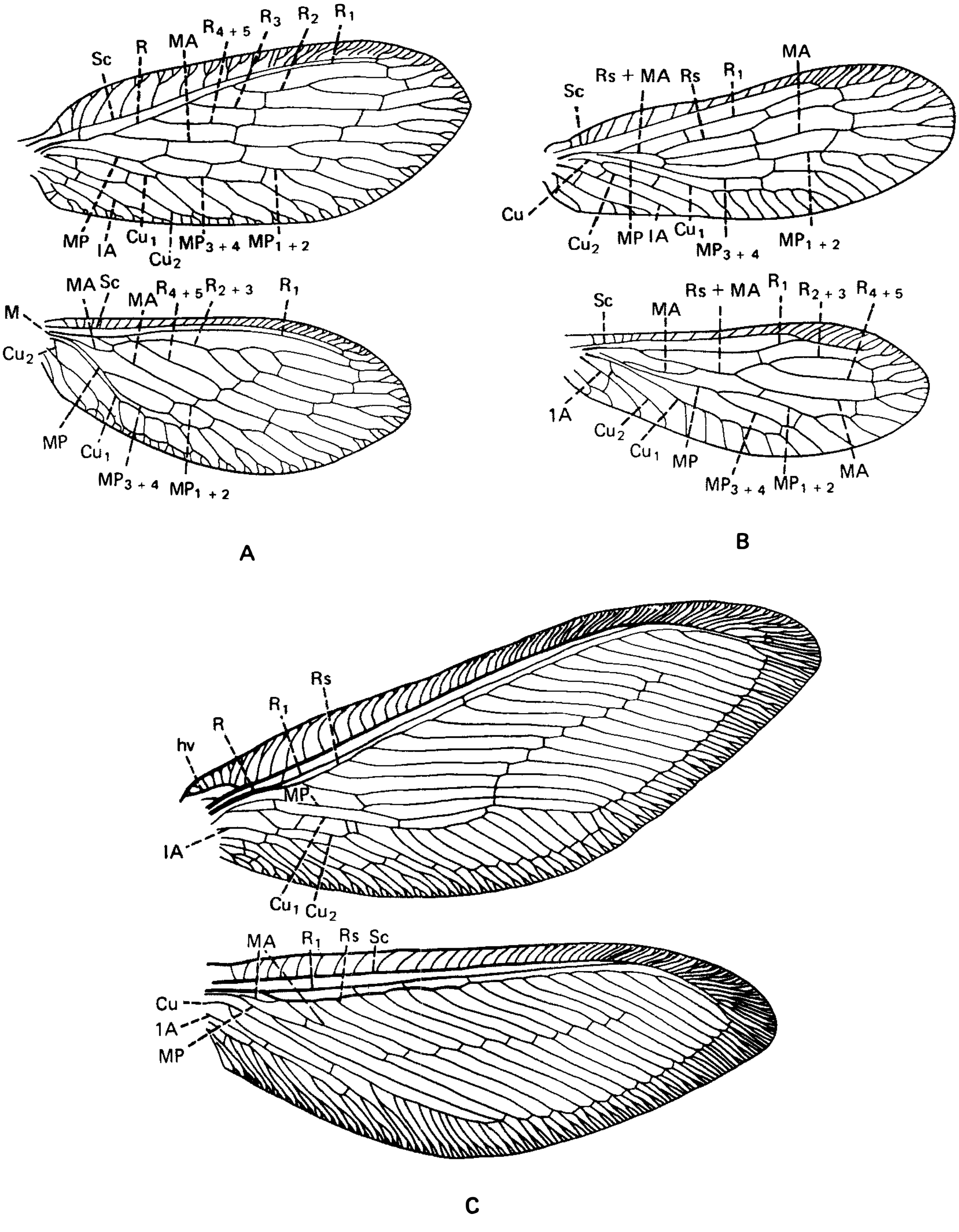


Figure 27–2 Wings of Neuroptera. A, *Ameromicromus* (Hemerobiidae); B, *Climacia* (Sisyridae); C, *Polystoechotes* (Polystoechotidae). The venation is labeled with the interpretation of Carpenter (1940) and others. *hv*, humeral or recurrent vein; MA, anterior media; MP, posterior media.

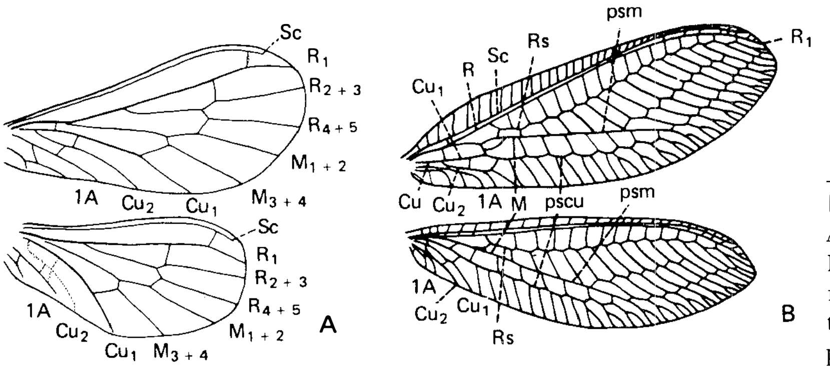


Figure 27–3 Wings of Neuroptera. A, *Coniopteryx* (Coniopterygidae); B, *Chrysopa* (Chrysopidae). The venation is labeled with the interpretation of Comstock (1940). *pscu*, pseudocubitus; *psm*, pseudomedia.

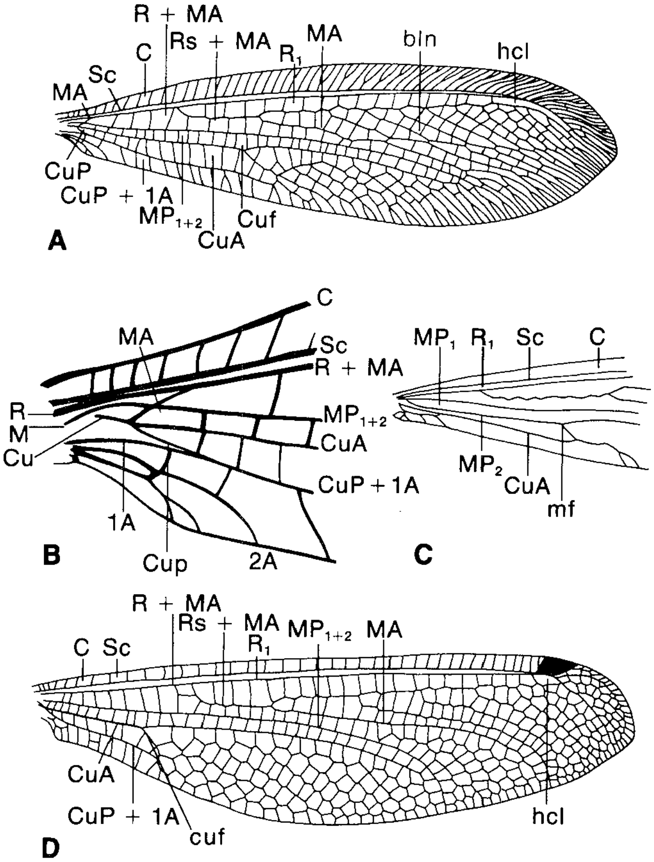


Figure 27–4 Wings of Myrmeleontoidea. A, front wing of *Dendroleon* (Myrmeleontidae); B, base of the same wing as A, enlarged to show detail; C, base of hind wing of *Dendroleon*, with most crossveins not shown; D, front wing of an ascalaphid. *bln*, banksian line; *cuf*, cubital fork (fork of CuA); *hcl*, hypostigmatic or truss cell; *mf*, medial fork (fork of MP_2).

7(4′). Antennae clubbed or knobbed; insects with abdomen long and slender, resembling dragonflies or damselflies in general appearance (Figure 27–10) (superfamily Myrmeleontoidea) 8

7′. Antennae filiform, moniliform, or pectinate, not clubbed or knobbed; usually not particularly resembling dragonflies or damselflies in appearance 9

8(7). Antennae about as long as head and thorax together (Figure 27–10); hypostigmatic cell (cell behind the point of fusion of Sc and R_1; Figure 27–4A, hcl) very long, several times as long as wide; eyes entire Myrmeleontidae p. 478

8′.	Antennae nearly or quite as long as body; hypostigmatic cell short, not more than 2 or 3 times as long as wide (Figure 27–4D, *hcl*); eyes entire (Haplogleninae) or divided horizontally (Ascalaphinae)	Ascalaphidae	p. 479
9(7′).	At least some, usually many, costal crossveins forked (Figure 27–2A,C)	10	
9′.	All (or nearly all) costal crossveins simple (Figures 27–2B and 27–3B)	13	
10(9).	Front wings apparently with 2 or more radial sectors (Figure 27–2A: R$_2$, R$_3$, R$_{4+5}$)	Hemerobiidae	p. 477
10′.	Front wings with only 1 radial sector, which has 2 or more branches (Figure 27–2C, Rs)	11*	
11(10′).	Front wings with a recurrent humeral vein (Figure 27–2C, *hv*), 16–34 mm long	12*	
11′.	Front wings without a recurrent humeral vein, 9–13 mm long	Berothidae*	p. 477
12(11).	Sc and R$_1$ in front wing fused distally; Rs in front wing with many branches, crossveins between them forming a fairly distinct gradate vein; free basal portion of MA in hind wing longitudinal (Figure 27–2C); widely distributed	Polystoechotidae*	p. 478
12′.	Sc and R$_1$ in front wing not fused distally; Rs in front wing with only a few branches, crossveins between them scattered and not forming a distinct gradate vein; free basal part of MA in hind wing short and oblique; southern California	Ithonidae*	p. 476
13(9′).	Sc and R$_1$ in front wing not fused near wing tip, Rs appearing unbranched (Figure 27–3B); wings, at least in life, often greenish; very common insects	Chrysopidae	p. 477
13′.	Sc and R$_1$ in front wing fused or separate apically, Rs appearing branched (Figure 27–2B); wings not greenish; uncommon insects	14	
14(13′).	Antennae pectinate in male, filiform in female; female with exserted ovipositor about as long as body; hind wing about as long as front wing in male, about two-thirds as long as front wing in female; front wing 3.0–5.5 mm long	Dilaridae*	p. 477
14′.	Antennae filiform in both sexes; female without exserted ovipositor; hind wing with free basal part of MA present, longitudinal (Figure 27–2B); wings elongate-oval, hind wing nearly as long as front wing; front wing 3.4–7.0 mm long	Sisyridae	p. 478

SUBORDER **Megaloptera:** The members of the suborder Megaloptera have the hind wings broader at the base than the front wings, and this enlarged anal area is folded fanwise at rest. The longitudinal veins do not have branches near the wing margin, as do those of many of the other insects in this order. Ocelli may be present or absent. The larvae are aquatic, with lateral abdominal gills, and with normal jaws (not elongate and sicklelike, as in the Planipennia). The pupae are not in cocoons.

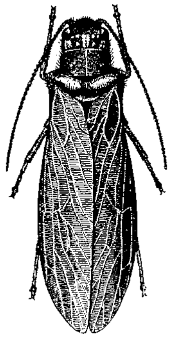


Figure 27–5 An alderfly, *Sialis mohri* Ross. (Courtesy of the Illinois Natural History Survey.)

Family **Sialidae—Alderflies:** The alderflies (Figure 27–5) are dark-colored insects, about 25 mm long or less, and are usually found near water. The adults are generally similar to corydalids, but are smaller and lack ocelli. The larvae are aquatic and are usually found

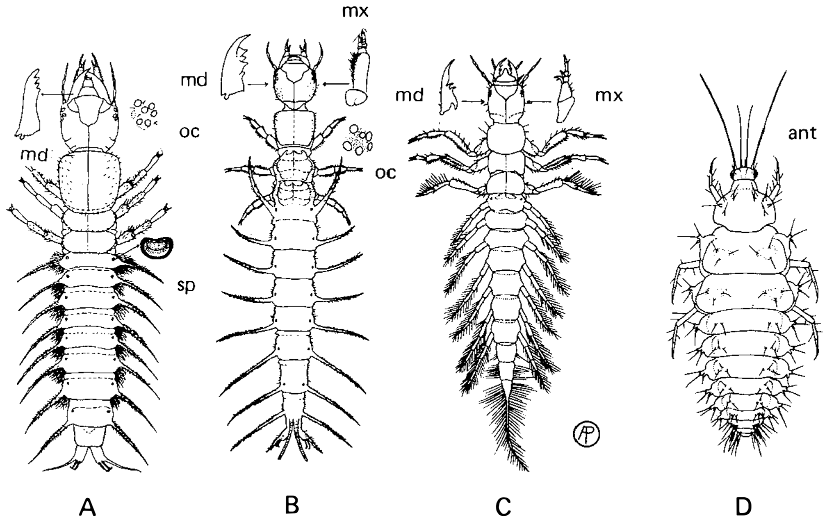


Figure 27–6 Larvae of aquatic Neuroptera; A, *Corydalus* (Corydalidae); B, *Chauliodes* (Corydalidae); C, *Sialis* (Sialidae); D, *Climacia* (Sisyridae). *ant*, antenna; *md*, mandible; *mx*, maxilla; *oc*, ocelli; *sp*, spiracle. (Courtesy of Peterson. Reprinted by permission.)

under stones in streams. They are predaceous on small aquatic insects. The larvae of alderflies (Figure 27–6C) differ from those of the Corydalidae in that they have a terminal filament, seven pairs of lateral filaments, and no hooked anal prolegs. *Sialis infumata* Newman is a common eastern species that is about 19 mm long and has smoky wings. There are 24 species of alderflies in the United States, all in the genus *Sialis*.

Family **Corydalidae—Dobsonflies and Fishflies:** These insects are similar to the alderflies, but are in general larger (usually over 25 mm long) and have ocelli. They are soft-bodied, have a rather fluttery flight, and are usually found near water. Some species are attracted to lights and may be found some distance from water. The larvae (Figure 27–6A,B) are aquatic and usually live under stones in streams. They differ from alderfly larvae in that they have a pair of hooked anal prolegs, no terminal filament, and eight pairs of lateral filaments. These larvae are sometimes called "hellgrammites" and are frequently used as bait by fisherman. The jaws can inflict a painful nip.

The largest insects in this group are the dobsonflies (*Corydalus* and *Dysmicohermes*), which have front wings 50 mm or more long. A common eastern species (Figure 27–7) has a wingspread of about 130 mm, and the males have extremely long mandibles. The smaller

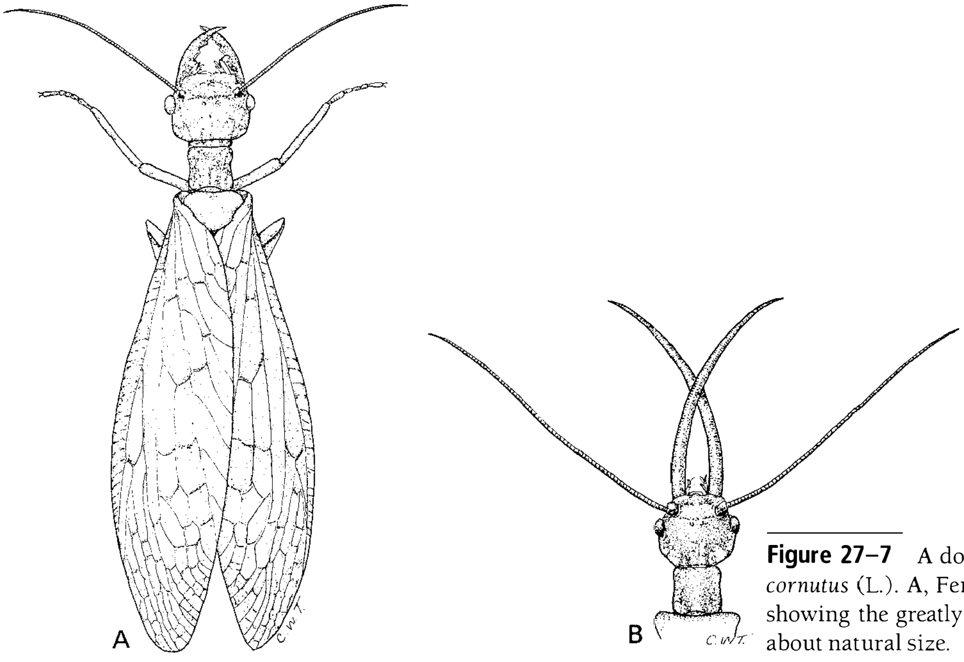


Figure 27–7 A dobsonfly, *Corydalus cornutus* (L.). A, Female; B, head of male showing the greatly enlarged mandibles; about natural size.

species in this group (front wings less than 50 mm long) are called "fishflies." Most belong to the genera *Chauliodes*, *Neohermes*, and *Nigronia*. Dobsonflies and some of the fishflies have clear wings, but other fishflies (species of *Nigronia*) have black or smoky wings with a few small, clear areas. Fishflies in the genera *Chauliodes* and *Nigronia* have serrate or pectinate antennae. In the United States there are 24 species in seven genera of Corydalidae.

SUBORDER **Raphidioptera:** The insects of the suborder Raphidioptera are peculiar in having the prothorax elongate, somewhat as in the Mantispidae, but the front legs are similar to the other legs and arise from the posterior end of the prothorax (Figure 27–8A). These insects can raise their head above the rest of the body, much like a snake preparing to strike. The adults are predaceous, but can catch only small, weak prey. The female (which has a long ovipositor) lays her eggs in clusters in crevices in bark, and the larvae are usually found under bark. The larvae feed principally on small insects such as aphids and caterpillars. The snakeflies occur only in the western states.

Family **Raphidiidae:** This family is represented in North America by 17 species of *Agulla* and 2 of *Alena*, which are widely distributed through the West, from central Texas and California north to British Columbia and Alberta. They vary in size, with the front wings ranging from 6 to 17 mm long. Females are usually a little larger than males.

Family **Inocelliidae:** This group is represented in North America by three species of *Negha*, which occur from California and Nevada north to British Columbia. Inocelliids are larger than most raphidiids, with the front wing varying in length from 11 to 17 mm. They also have longer and thicker antennae and a larger, darker pterostigma than raphidiids.

SUBORDER **Planipennia:** This suborder includes the dusty-wings, lacewings, antlions, and owlflies. Some authorities include only these insects in the order Neuroptera. The adults lack ocelli, the front and hind wings (in North American species) are similar in size and shape, and the longitudinal veins in the wings often have branches near the wing margin. The larvae have long sicklelike mandibles, and the food is sucked up through a channel formed between the mandible and maxilla. Pupation occurs in a silken cocoon.

Family **Coniopterygidae—Dusty-Wings:** These are minute insects, 3 mm long or less, and are covered with a whitish powder. There are 55 species in eight genera in North America, and most are relatively rare. The larvae feed on small insects and insect eggs.

Family **Ithonidae:** This family is represented in the United States by a single, uncommon species, *Oliarces clara* Banks, which has been taken in southern California. This insect has a wingspread of 35–40 mm and resembles a *Sialis* with bleached wings. The larvae are scarabaeiform and probably feed on creosote bush. Adults have "hill-topping" behavior and can be en-

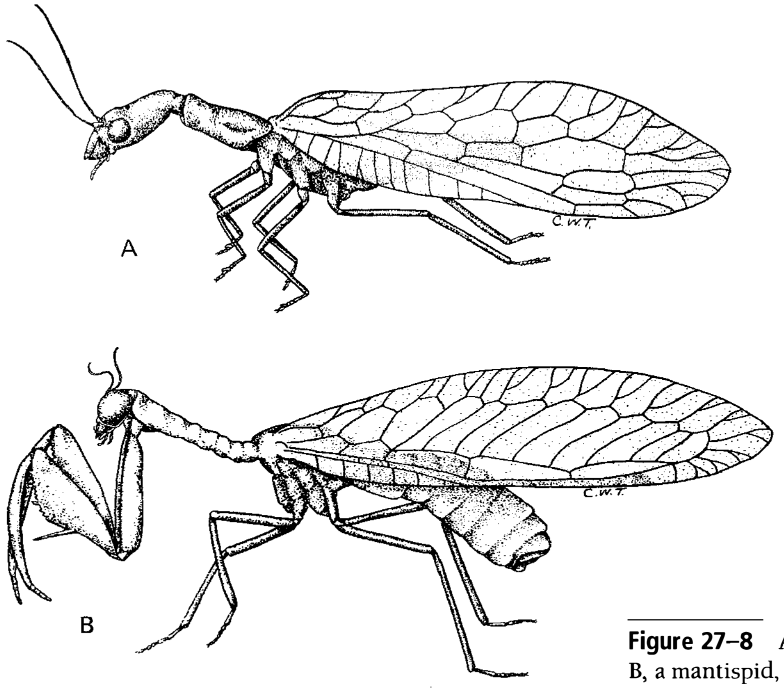


Figure 27–8 A, a snakefly, *Raphidia adnixa* (Hagen); B, a mantispid, *Mantispa cincticornis* Banks.

countered on high places in mass emergences. When alive, adults have greenish-blue bodies.

Family **Mantispidae—Mantidflies:** These insects resemble mantids in having a lengthened prothorax and front legs enlarged and fitted for grasping prey (Figure 27–8B). They have a wingspread of 25 mm or so. The larvae of some species (such as *Plega*) feed primarily on the larvae of wasps and bees, whereas those of other species (such as *Mantispa* and *Climaciella*) feed on spider eggs. Mantidflies undergo hypermetamorphosis: The first-instar larvae are active and campodeiform, and the subsequent larval insects are scarabaeiform. These insects are more common in the South. There are 14 species, in seven genera, known from the United States.

Family **Hemerobiidae—Brown Lacewings:** These insects resemble common lacewings (Chrysopidae), but are brownish instead of green and generally smaller, and they have a different wing venation. The chrysopids have a single distinct radial sector, whereas the hemerobiids appear to have from two to four or more (that is, two to four veins branch off R_1). Most hemerobiids appear to have three or four radial sectors. Some species have a recurved and branched humeral vein in the front wing. Brown lacewings are generally found in wooded areas, and are much less common than the Chrysopidae. The eggs, which are not stalked, are laid on plants. The larvae are predaceous. This is the third largest family in the order, with 61 North American species in 6 genera.

Family **Chrysopidae—Common Lacewings:** This is the second largest family in the order (84 North American species in 15 genera), and its members are common insects—usually living in grass and weeds and on the foliage of trees and shrubs. Most are greenish, with copper-colored eyes (Figure 27–9A). The species of *Eremochrysa* (western) are often tan and resemble hemerobiids. Some chrysopids give off a rather disagreeable odor when handled. The larvae of most species are predaceous, chiefly on aphids, and are sometimes called "aphidlions" (Figure 27–9B). Some larvae pile debris on their backs and carry it around. The adults may be predaceous (such as *Chrysopa*), feed on pollen (such as *Meleoma*), or feed on honeydew (such as *Eremochrysa*). The eggs are usually laid on foliage, the female produces a thin, elongate stalk and attaches the egg at its end (Figure 27–9C). The larvae pupate in silken cocoons that are generally attached to the underside of leaves. In late autumn adults of *Chrysoperla* migrate in large numbers to the forest, where they overwinter.

Family **Dilaridae—Pleasing Lacewings:** This group contains two rare North American species. *Nallachius americanus* (MacLachlan), which has MP in the front wing forked near the wing margin, has been recorded from several eastern states, from Michigan to Georgia; *N. pulchellus* (Banks), which has MP in the front wing forked near its base, has been recorded from Cuba and Arizona. Unlike most Neuroptera, these insects commonly rest with the wings outspread and resemble small moths. The female's ovipositor is a little longer than her body. Males have plumose antennae. The eggs are laid in crevices or under bark, and the larvae are predaceous.

Family **Berothidae—Beaded Lacewings:** This family is represented in North America by 10 rather rare species in the genus *Lomamyia*. Adults are frequently attracted to lights at night and resemble slender cad-

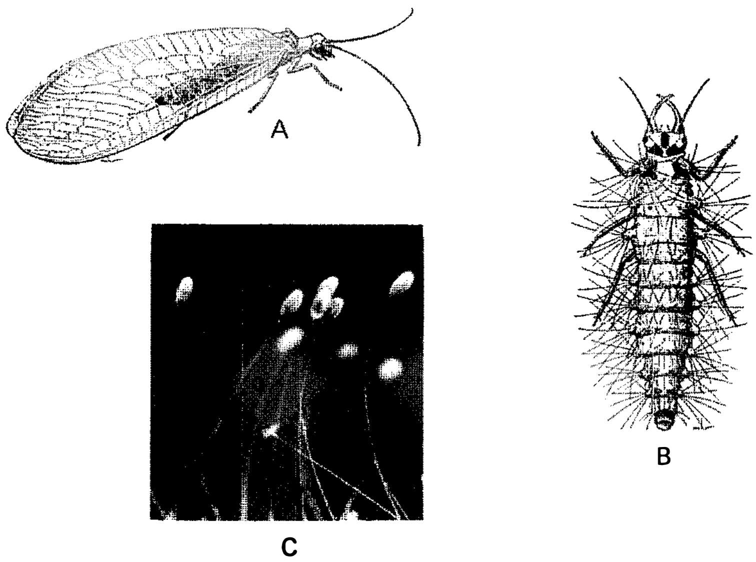


Figure 27–9 Adult (A), larva (B), and eggs (C) of a common lacewing, *Chrysopa* sp. (A and B, courtesy of the Illinois Natural History Survey.)

disflies. In some species the outer margin of the front wing is somewhat indented just behind the apex, and the females of some species have scales on the wings and thorax. The eggs are stalked. The larvae are predaceous on termites.

Family **Polystoechotidae—Giant Lacewings:** These lacewings have a wingspread of 40–75 mm. They are quite rare, and only two species are known in North America. The more common species, *Polystoechotes punctatus* (Fabricius), is attracted to smoke; this species has disappeared from the eastern half of the United States in the last 50 years for unknown reasons. Even in the West it is becoming more uncommon.

Family **Sisyridae—Spongillaflies:** The spongillaflies look very much like tiny, brownish lacewings. They are usually found near ponds or streams, because the larvae (Figure 27–6D) are aquatic and feed on freshwater sponges. When full grown, the larvae emerge from the water and pupate in silken cocoons attached to objects near the water. These cocoons are constructed inside hemispherical cocoon covers.

There are six species of spongillaflies in North America, three in each of the genera *Climacia* and *Sisyra*. These genera differ in the forking of Rs. *Climacia* has a single fork in Rs, located below the pterostigma (Figure 27–2B), and *Sisyra* has two forks in this vein, located well proximad of the pterostigma. *Climacia* are pale with dark markings, whereas *Sisyra* are a uniform smoky brown.

Family **Myrmeleontidae—Antlions:** This is the largest family in the order (92 North American species in 13 genera). Its members are widely distributed, but are most abundant in the South and West and a little less common in the northern part of the United States. The adults of this group resemble damselflies, with a long, slender abdomen (Figure 27–10). They differ from damselflies in being softer-bodied; in having relatively long, clubbed antennae; and in having quite different wing venation (compare Figures 27–4A and 10–6). They are rather feeble fliers and are often attracted to lights. The wings are clear in some species and irregularly spotted in others (Figure 27–10).

Antlion larvae, or "doodlebugs," are rounded creatures with long, sicklelike jaws (Figure 27–11A). Most (Acanthoclisini and Dendroleontini) either lie in wait for their prey on the surface of the ground (generally in sandy areas) or buried just beneath the surface, or they give chase on the surface. Most larvae move both for-

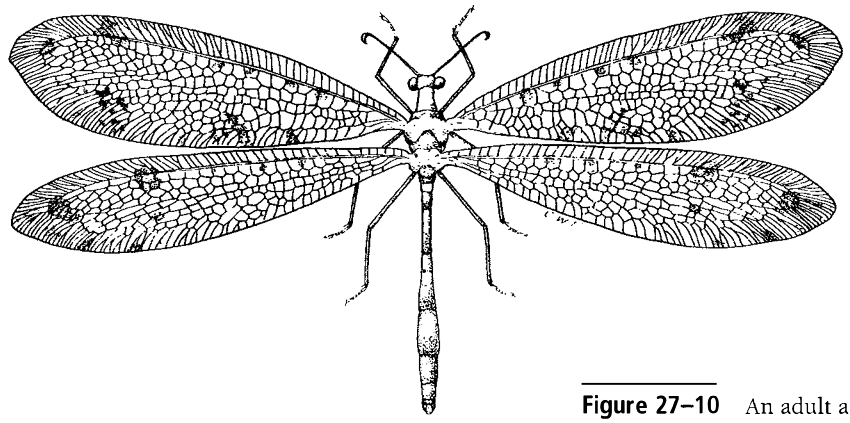


Figure 27–10 An adult antlion, *Dendroleon obsoletum* (Say).

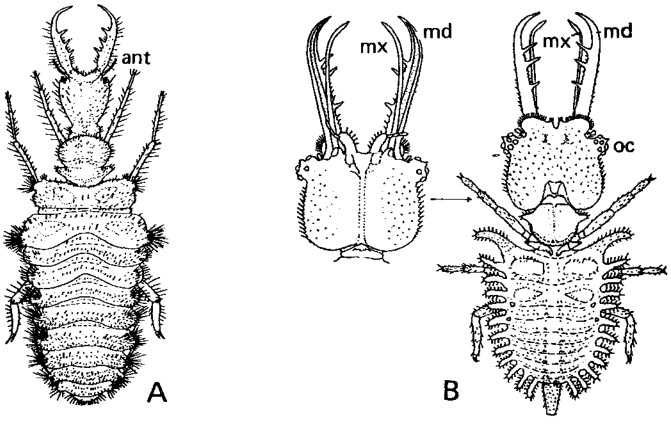


Figure 27–11 Larvae of Myrmeleontoidea. A, *Myrmeleon immaculatus* DeGeer (Myrmeleontidae); B, *Ascaloptynx appendiculatus* (Fabricius) (Ascalaphidae). *ant*, antennae; *md*, mandible; *mx*, maxilla; *oc*, ocelli. (Courtesy of Peterson. Reprinted by permission.)

ward and backward equally well. Some species in this family (the Myrmeleontini) capture their prey by means of pitfalls. They conceal themselves in the bottom of a small, conical pit, made in sand or dust, and feed on ants and other insects that fall into this pit. The pits are generally 35–50 mm across and are usually found in dry situations such as under cliff overhangs or under buildings. It is not always easy to dig one of these larvae from its pit, because the larvae remain motionless when disturbed and, when dug up, are covered with a layer of sand or dust and are easily overlooked. Antlion larvae pupate in the soil, in a cocoon made of sand and silk.

This group contains several distinctive venational features, some of which are of taxonomic value: (1) a characteristic fork in the basal third of the wing (the trigonal fork of Comstock), formed by the forking of the CuA in the front wing and of MP_2 in the hind wing; (2) the prefork area (the trigonal loop of Comstock), the area between MP_2 and CuA+1A in the front wing; (3) the hypostigmatic cell (the truss cell of Comstock), a long cell behind the point of fusion of Sc and R_1 in the distal part of the wing (Figure 27–4, hcl); and (4) the presectoral crossveins, those basad of the separation of Rs+MA from R_1, extending between Rs+MA and MP in the front wing and between Rs+MA and MP_1 in the hind wing. Some species have a fairly distinct gradate vein called the *banksian line*, extending lengthwise of the wing in the distal half or third of the wing (Figure 27–4A, bln).

The North American species of antlions are arranged in six tribes of the subfamily Myrmeleontinae: Acanthoclisini, Brachynemurini, Dendroleontini, Gnopholeontini, Myrmeleontini, and Nemoleontini. The Acanthoclisini and Gnopholeontini occur only in the West, but the other four tribes are widely distributed. Only the larvae of the Myrmeleontini construct pitfalls.

***Family* Ascalaphidae—Owlflies:** These large, dragonfly-like insects have long, clubbed antennae. They are fairly common in the South and Southwest, but are quite rare in the North. Most species lay their eggs on twigs, and a week or so after hatching the larvae climb down to the ground, where they live in litter. The larvae of a few species may be arboreal. Some larvae cover themselves with debris; others have a coloration that renders them inconspicuous. The larvae are predaceous. They lie in wait for their prey with their large jaws wide open. The closing of the jaws on a prey is apparently triggered by contact, and the prey is usually paralyzed within seconds by the bite of the ascalaphid larva. Pupation occurs in litter, in a silken cocoon, and lasts from a few weeks to a few months. Some adults are diurnal, and some are nocturnal. Most North American species fly at dusk, flying up to 10 m above the ground by the time of complete darkness. The flight of the adults is strong and dragonfly-like, with periods of hovering and rapid flight, the adults feeding on small insects. Adults spend much of their time resting—usually head down on a vertical twig, with the body projecting from the twig at about a right angle—thus resembling a small twig. They apparently cannot fly off directly from a resting position, but warm up for several minutes, vibrating their wings. The adults of some species develop some color in the wings a few days after emergence. There are 6 species, in two genera, in North America.

Collecting and Preserving Neuroptera

Most Neuroptera can be collected with an insect net by sweeping vegetation. Adults of the Sialidae, Corydalidae, and Sisyridae are generally found near the aquatic habitats (ponds and streams) in which the larvae live. The best way to collect many Neuroptera, particularly representatives of the less common groups, is at lights. Polystoechotidae can be collected by building smoky fires in remote areas in late autumn.

Adult Neuroptera are preserved in alcohol, or on pins or points, or in envelopes. All are relatively soft-bodied, and pinned specimens often sag or shrivel and become distorted. Many pinned specimens need some support for the abdomen, at least until the insect has dried. Very small forms can be mounted on points, but preservation in alcohol is better. Large, elongate forms, such as dobsonflies and antlions, can be preserved in envelopes.

References

Adams, P. A. 1956. New antlions from the southwestern United States (Neuroptera: Myrmeleontidae). Psyche 63:82–108.

Aspöck, U. 1975. The present state of knowledge on the Rhaphidioptera of America (Insecta: Neuropteroidea). Polskie Pismo Entomol. 45:537–546.

Aspöck, H., U. Aspöck, and H. Rausch. 1991. Die Raphidioptera der Erde. Eine monographische Darstellung der Systematik, Taxonomie, Biologie, Oekologie und Corologie der rezenten Raphidopteren der Erde, mit einer zusammenfassender Uebersicht der fossilen Raphidiopteren (Insecta: Neuropteroidea). Vol. 1, 730 pp., Vol. 2, 550 pp. Krefeld, Germany: Goecke and Evers.

Aspöck, U., J. D. Plant, and H. L. Nemeschkal. 2001. Cladistic analysis of Neuroptera and their systematic position within Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). Syst. Entomol. 26:73–86.

Banks, N. 1927. Revision of Nearctic Myrmeleontidae. Bull. Mus. Comp. Zool. Harvard 68:1–84.

Bickley, W. E., and E. G. MacLeod. 1956. A synopsis of the Nearctic Chrysopidae with a key to the genera (Neuroptera). Proc. Entomol. Soc. Wash. 58:177–202.

Brooks, S. J., and P. C. Barnard. 1990. The green lacewings of the world: a generic revision (Neuroptera: Chrysopidae). Bull. Brit. Mus. (Nat. Hist.) Entomol. 59:117–286.

Carpenter, F M. 1936. Revision of the Nearctic Raphidiodea (recent and fossil). Proc. Amer. Acad. Arts Sci. 71(2):89–157.

Carpenter, F. M. 1940. A revision of the nearctic Hemerobiidae, Berothidae, Sisyridae, Polystoechotidae, and Dilaridae (Neuroptera). Proc. Amer. Acad. Arts Sci. 74(7):193–280.

Carpenter, F. M. 1951. The structure and relationships of *Oliarces* (Neuroptera). Psyche 58:32–41.

Chandler, H. P. 1956. Megaloptera. In R. L. Usinger (Ed.), Aquatic Insects of California, pp. 229–233. Berkeley: University of California Press.

Comstock, J. H. 1940. An introduction to entomology. Ninth edition. Ithaca, NY: Comstock Publishing Company, Inc. 1064 p.

Froeschner, R. C. 1947. Notes and keys to the Neuroptera of Missouri. Ann. Entomol. Soc. Amer. 40:123–136.

Glorioso, M. J. 1981. Systematics of the dobsonfly subfamily Corydalinae (Megaloptera: Corydalidae). Syst. Entomol. 6:253–290.

Gurney, A. B. 1947. Notes on Dilaridae and Berothidae, with special reference to the immature stages of the Nearctic genera (Neuroptera). Psyche 54:145–169.

Gurney, A. B., and S. Parfin. 1959. Neuroptera. In W. T. Edmondson (Ed.), Freshwater Biology, pp. 973–980. New York: Wiley.

Henry, C. S. 1977. The behavior and life histories of two North American ascalaphids. Ann. Entomol. Soc. Amer. 70:176–195.

Hoffman, K. M. 2002. Mantispidae. In N. D. Penny (Ed.), A guide to the lacewings (Neuroptera) of Costa Rica. Proc. Calif. Acad. Sci. 53(12):161–457.

Johnson, J. B., and K. S. Hagen. 1981. A neuropterous larva uses an allomone to attack termites. Nature 289:506–507.

Lambkin, K. J. 1986a. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family. Part 1: General and Drepanicinae. Austral. J. Zool., Suppl. Ser. 116:1–142.

Lambkin, K. J. 1986b. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family. Part 2: Calomantispinae and Mantispinae. Austral. J. Zool., Suppl. Ser. 117:1–113.

MacLeod, E. G., and K. E. Redborg. 1982. Larval platymantispine mantispids (Neuroptera: Planipennia): Possibly a subfamily of general predators. Neuroptera Int. 2:37–41.

Martynov, A. 1928. Permian fossil insects of northeast Europe. Trav. Mus. Geol. Acad. Sci. USSR 4:1–117.

Meinander, M. 1972. A revision of the family Coniopterygidae. Acta Zool. Fenn. 136:1–357.

Nakahara, W. 1965. Contribution to the knowledge of the Hemerobiidae of western North America (Neuroptera). Proc. U.S. Nat. Mus. 116:205–222.

Neunzig, H. H., and J. R. Baker. 1991. Order Megaloptera. In F. W. Stehr (Ed.), Immature insects, vol. 2, pp. 112–122. Dubuque, IA:. Kendall/Hunt, 975 pp.

Oswald, J. D. 1993. Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). J. N. Y. Entomol. Soc. 101:143–299.

Oswald, J. D., and N. D. Penny. 1991. Genus-group names of the Neuroptera, Megaloptera, and Raphidioptera of the world. Occ. Pap. Calif. Acad. Sci. 147:1–94.

Parfin, S. 1952. The Megaloptera and Neuroptera of Minnesota. Amer. Midl. Nat. 47(2):421–434.

Parfin, S., and A. B. Gurney. 1956. The spongillaflies with special reference to those of the western hemisphere (Sisyridae, Neuroptera). Proc. U.S. Natl. Mus. 105(3360):421–529.

Penny, N. D., P. A. Adams, and L. A. Stange. 1997. Species catalog of the Neuroptera, Megaloptera, and Rhaphidioptera of America north of Mexico. Proc. Calif. Acad. Sci. 50:39–114.

Penny, N. D., C. A. Tauber, and T. de Leon. 2000. A new species of *Chrysopa* from western North America with a key to North American species (Neuroptera: Chrysopidae). Ann. Entomol. Soc. Amer. 93:776–784.

Redborg, K. E., and E. G. MacLeod. 1985. The developmental ecology of *Mantispa uhleri* Banks (Neuroptera: Mantispidae). Ill. Biol. Monogr. No. 53. Champaign, IL: University of Illinois Press, 130 pp.

Rehn, J. W. H. 1939. Studies in North American Mantispidae (Neuroptera). Trans. Amer. Entomol. Soc. 65:237–263.

Ross, H. H. 1937. Nearctic alderflies of the genus *Sialis*. Ill. Nat. Hist. Surv. Bull. 21(3):57–78.

Smith, R. C. 1922. The biology of the Chrysopidae. N.Y. (Cornell) Agr. Expt. Sta. Mem. 58:1285–1377.

Stange, L. A. 1970. Revision of the antlion tribe Brachynemurini of North America (Neuroptera: Myrmeleontidae). Univ. Calif. Publ. Entomol. 55:1–192.

Stange, L. A. 1994. Reclassification of the New World antlion genera formerly included in the tribe Brachynemurini (Myrmeleontidae). Insecta Mundi 8:67–119.

Tauber, C. A. 1969. Taxonomy and biology of the lacewing genus *Meleoma* (Neuroptera: Chrysopidae). Univ. Calif. Publ. Entomol. 58:1–94.

Tauber, C. A. 1991a. Order Raphidioptera.In F. W. Stehr (Ed.), Immature insects, vol. 2, pp. 123–125. Dubuque, IA: Kendall/Hunt, 975 pp.

Tauber, C. A. 1991b. Order Neuroptera. In F. W. Stehr (Ed.), Immature insects, vol. 2, pp. 126–143. Dubuque, IA: Kendall/Hunt, 975 pp.

Throne, A. L. 1971a. The Neuroptera—suborder Planipennia of Wisconsin. Part 1: Introduction and Chrysopidae. Mich. Entomol. 4(3):65–78.

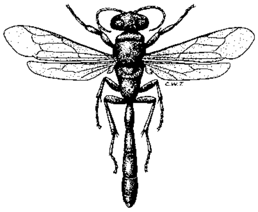
Throne, A. L. 1971b. The Neuroptera—suborder Planipennia of Wisconsin. Part 2: Hemerobiidae, Polystoechotidae, and Sisyridae. Mich. Entomol. 4(3):79–87.

Withycombe, C. L. 1925. Some aspects of the biology and morphology of the Neuroptera, with special reference to the immature stages and their phylogenetic significance. Trans. Entomol. Soc. Lond. 1924:303–411.

28

Order Hymenoptera[1]

Sawflies, Parasitic Wasps, Ants, Wasps, and Bees



From the human standpoint, this order is probably the most beneficial in the entire insect class. It contains a great many species that are of value as parasites or predators of insect pests, and it contains the most important pollinators of plants, the bees. The Hymenoptera are a very interesting group in terms of their biology, because they exhibit a great diversity of habits and complexity of behavior culminating in the social organization of the wasps, bees, and ants.

The winged members of this order have four membranous wings. The hind wings are smaller than the front wings and have a row of tiny hooks (hamuli) on their anterior margin, by which the hind wing attaches to a fold on the posterior edge of the front wing. The wings contain relatively few veins, and some minute forms have no veins at all. The mouthparts are mandibulate, but in many, especially the bees, the labium and maxillae form a tonguelike structure through which liquid food is taken (Figure 28–6). The antennae usually contain 10 or more segments and are generally fairly long. The tarsi usually have five segments. The ovipositor is generally well developed. In some cases it is modified into a sting, which functions as an organ of offense and defense. Because the sting is derived from an egg-laying organ, only females can sting. The metamorphosis is complete, and in most of the order, the larvae are grublike or maggotlike. The larvae of most sawflies and related forms are eruciform and differ from those of the Lepidoptera in that they have more than five pairs of prolegs, lack crochets on these prolegs, and usually have only a single pair of ocelli. The pupae are exarate and may be formed in a cocoon, within the host (in the case of parasitic species), or in special cells.

Sex in most Hymenoptera is associated with the fertilization of the egg. Fertilized eggs develop into females, and unfertilized eggs usually develop into males.

Classification of the Hymenoptera

The order Hymenoptera was traditionally divided into two suborders, the Symphyta (or Chalastogastra) and the Apocrita. Nearly all symphytes are phytophagous. Entomologists now widely accept that the Symphyta is, in fact, a paraphyletic group. In the suborder Apocrita, the basal segment of the abdomen is fused with the thorax and separated from the remainder of the abdomen by a constriction. The abdominal segment that is fused with the thorax is called the *propodeum*. The resulting four-segmented locomotory tagma is known as the *mesosoma* (or trunk). The posterior tagma is the *metasoma* (or gaster). The trochanters appear one- or two-segmented in the Apocrita, and there are no more than two closed cells at the base of the hind wing (Figure 28–2). The larvae of most species of Apocrita feed on other arthropods, although phytophagy has re-evolved several times.

A synopsis of the order Hymenoptera is given in the following list. Alternate spellings, synonyms, and other arrangements are given in parentheses. The higher classification of the order is in a state of flux. The arrangement presented here follows in broad outline that of Brothers (1975), Krombein et al. (1979), Rasnitsyn (1980), and Goulet and Huber (1993). The

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[1] Hymenoptera: *hymeno*, god of marriage; *ptera*, wings (referring to the union of front and hind wings by means of hamuli).

groups marked with an asterisk (*) are relatively rare or are unlikely to be taken by a general collector.

- Superfamily Xyeloidea
  - Xyelidae*
- Superfamily Megalodontoidea
  - Pamphiliidae (Lydidae)—leaf-rolling and web-spinning sawflies*
- Superfamily Tenthredinoidea
  - Pergidae (Acorduleceridae)*
  - Argidae (Hylotomidae)
  - Cimbicidae (Clavellariidae)
  - Diprionidae (Lophyridae)—conifer sawflies
  - Tenthredinidae—common sawflies
- Superfamily Cephoidea
  - Cephidae—stem sawflies
- Superfamily Siricoidea
  - Anaxyelidae (Syntexidae, Syntectidae)—incense-cedar wood wasps*
  - Siricidae (Uroceridae)—horntails
  - Xiphydriidae—wood wasps*
- Superfamily Orussoidea
  - Orussidae (Oryssidae, Idiogastra)—parasitic wood wasps*
- Suborder Apocrita (Clistogastra, Petiolata)
  - Superfamily Stephanoidea
    - Stephanidae*
  - Superfamily Ceraphronoidea
    - Megaspilidae (Ceraphronidae in part, Calliceratidae in part)
    - Ceraphronidae (Calliceratidae in part)
  - Superfamily Trigonalyoidea
    - Trigonalyidae (Trigonalidae)*
  - Superfamily Evanioidea
    - Evaniidae—ensign wasps
    - Gasteruptiidae (Gasteruptionidae)
    - Aulacidae (Gasteruptiidae in part)
  - Superfamily Ichneumonoidea
    - Braconidae (including Aphidiidae)
    - Ichneumonidae (including Paxylommatidae = Hybrizontidae)
  - Superfamily Mymarommatoidea
    - Mymarommatidae*
  - Superfamily Chalcidoidea
    - Mymaridae—fairyflies
    - Trichogrammatidae
    - Eulophidae (including Elasmidae)
    - Tetracampidae*
    - Aphelinidae (Eulophidae in part, Encyrtidae in part)
    - Signiphoridae (Encyrtidae in part; Thysanidae)*
    - Encyrtidae
    - Tanaostigmatidae (Encyrtidae in part)*
    - Eupelmidae
    - Torymidae (Callimomidae; including Podagrionidae in part)
    - Agaonidae (Agaontidae, Torymidae in part)—fig wasps*
    - Ormyridae
    - Pteromalidae (including Cleonymidae in part, Chalcedectidae, Eutrichosomatidae, and Miscogastridae)
    - Eucharitidae (Eucharididae, Eucharidae)
    - Perilampidae
    - Eurytomidae—seed chalcids
    - Chalcididae (Chalcidae)
    - Leucospidae (Leucospididae)
  - Superfamily Cynipoidea
    - Ibaliidae*
    - Liopteridae*
    - Figitidae (Alloxystidae, Eucoilidae, Charipidae, Cynipidae in part)
    - Cynipidae—gall wasps
  - Superfamily Proctotrupoidea
    - Pelecinidae
    - Vanhorniidae (Proctotrupidae in part, Serphidae in part) *
    - Roproniidae*
    - Heloridae*
    - Proctotrupidae (Serphidae)
    - Diapriidae (including Ambositridae, Belytidae, Cinetidae)
  - Superfamily Platygastroidea
    - Scelionidae
    - Platygastridae (Platygasteridae)
  - Superfamily Chrysidoidea (= Bethyloidea)
    - Chrysididae (including Cleptidae)—cuckoo wasps
    - Bethylidae
    - Dryinidae
    - Embolemidae (Dryinidae in part)*
    - Sclerogibbidae*
  - Superfamily Apoidea
    - Sphecidae (including Ampulicidae, Pemphredonidae, Astatidae, Crabronidae, Mellinae, Nyssonidae, Philanthidae)—mud-daubers, thread-waisted wasps
    - Melittidae*
    - Colletidae (including Hylaeidae)—plasterer and yellow-faced bees
    - Halictidae—sweat bees
    - Andrenidae (including Oxaeidae)
    - Megachilidae—leaf-cutting bees
    - Apidae (including Anthophoridae, Nomadidae, Euceridae, Ceratinidae, Xylocopidae, Bombidae)—honey bees, bumble bees, orchid bees, cuckoo bees, digger bees, and carpenter bees

- Superfamily Vespoidea
  - Tiphiidae (including Thynnidae)
  - Sierolomorphidae*
  - Sapygidae*
  - Mutillidae (including Myrmosinae)—velvet ants
  - Bradynobaenidae (Mutillidae in part)*
  - Pompilidae (Psammocharidae)—spider wasps
  - Rhopalosomatidae (Rhopalosomidae)*
  - Scoliidae
  - Vespidae (including Eumenidae, Masaridae)—paper wasps, yellow jackets, hornets, mason wasps, potter wasps
  - Formicidae—ants

Characters Used in Identifying Hymenoptera

Wing Venation

Venational characters are used a great deal to separate the various groups of Hymenoptera. There are not many veins or cells in the hymenopteran wings, but homologizing this venation with that in other orders has proved to be a problem. There are two basic terminologies in use for the venation of the Hymenoptera: a traditional system using terms specific for the order (Figure 28–3) and one developed by Ross (1936) that attempted to homologize the venation with that of other insects. In this chapter we generally will use the modification of Ross's system by Richards (1977) to refer to veins (Figures 28–1, 28–2). In those groups with very reduced venation (Chalcidoidea and Proctotrupoidea especially), it is much simpler to refer to the veins by their relative positions (see Figure 28–19B). We also follow Michener's (1944) suggestions regarding the names of some cells, and use the positional terms *marginal* and *submarginal cells* (Figure 28–3, *MC, SM*).

Leg Characters

The leg characters used in identification are chiefly the number of trochanter segments, the number and form of the tibial spurs, and the form of the tarsal segments. The sawflies and some superfamilies of the Apocrita have two trochanter segments (Figure 28–32A). In fact, the so-called second trochanter is actually a basal subdivision of the femur and is never movably articulated distally. In the bees (Apoidea), the first segment

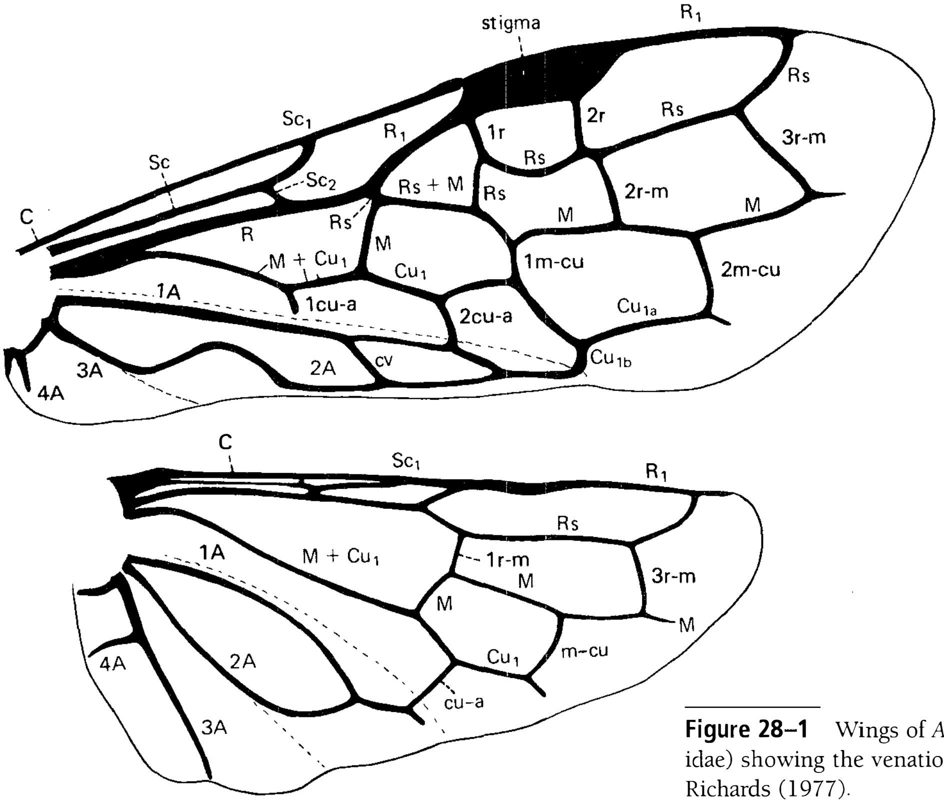

Figure 28–1 Wings of *Acantholyda* (Pamphiliidae) showing the venational terminology of Richards (1977).

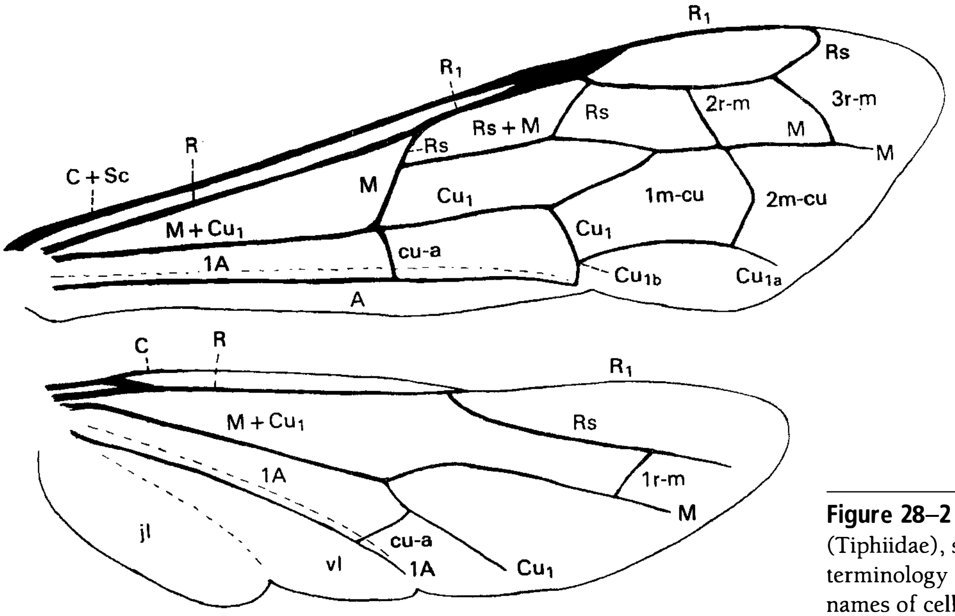

Figure 28–2 Wings of *Myzinum* (Tiphiidae), showing the venational terminology of Ross (1936) and the names of cells used in this book.

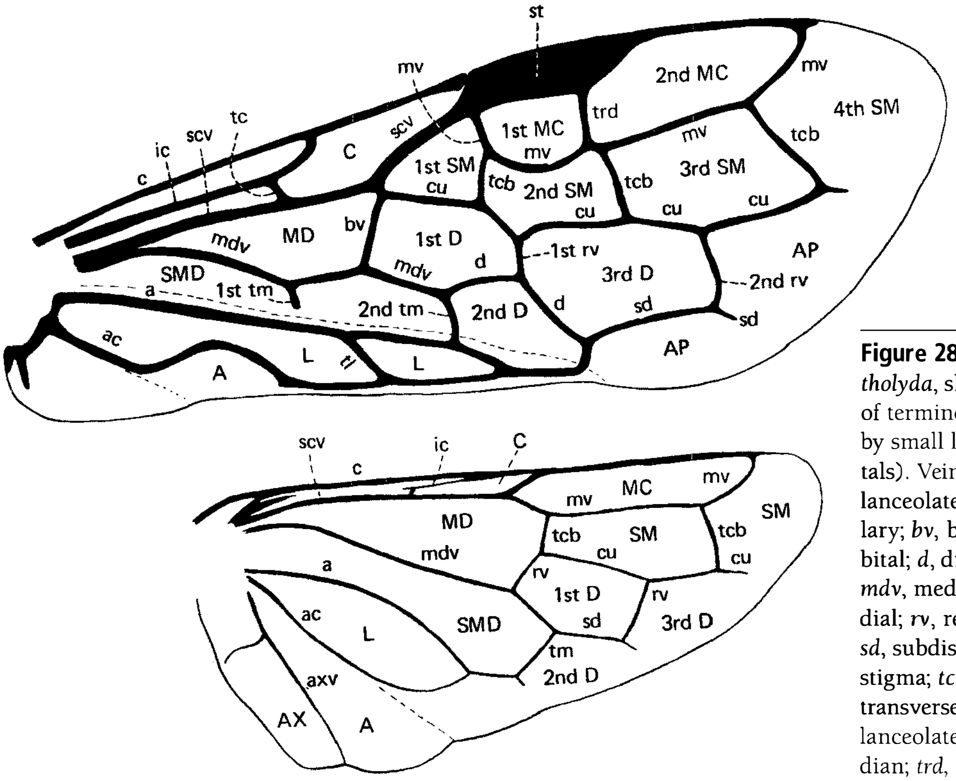

Figure 28–3 Wings of *Acantholyda*, showing the old system of terminology (veins are showed by small letters, cells by capitals). Veins: *a*, anal; *ac*, accessory, lanceolate, or subanal; *axv*, axillary; *bv*, basal; *c*, costal; *cu*, cubital; *d*, discoidal; *ic*, intercostal; *mdv*, median; *mv*, marginal or radial; *rv*, recurrent; *scv*, subcostal; *sd*, subdiscal or subdiscoidal; *st*, stigma; *tc*, transverse costal; *tcb*, transverse cubitals; *tl*, transverse lanceolate; *tm*, transverse median; *trd*, transverse radial or transverse marginal. Cells: *A*, anal; *AP*, apical or posterior; *AX*, axillary; *C*, costal; *D*, discoidal; *L*, lanceolate; *MC*, marginal; *MD*, median; *SM*, submarginal; *SMD*, submedian. The basal cells (hind wing) are *MD*, *SMD*, and *L*.

of the hind tarsus is usually much enlarged and flattened and may in some cases appear nearly as large as the tibia (Figure 28–15B,C). In some superfamilies, the size and shape of the hind coxae may help separate families.

Antennal Characters

The antennae of Hymenoptera vary in form, number of segments, and location on the face. In the Apocrita the number of antennal segments and, in some cases, the form of the antennae may differ in the two sexes. In most aculeates, the male has 13 antennal segments and the female has 12. In the ants, the antennae are much more distinctly elbowed in the queens and workers than in the males. In the Chalcidoidea, the antennal flagellum may be thought of as consisting of three sections (Figure 28–25B): an apical clava (*cva*), the ring segments basally (*rg*), and the funicle between the two (*fun*). The clava is formed of one to three segments that are distinguished by their close association rather than necessarily by any expansion. The ring segments (or anneli) are minute, reduced segments, sometimes only visible under a compound microscope. The key refers to the number of segments in the funicle. These are usually much longer than the ring segments and easily distinguished from them. In those few cases where it is unclear whether a segment represents a large ring segment or a small funicular segment, it should be included in the count of the latter.

Thoracic Characters

The thoracic characters used in identifying Hymenoptera involve principally the form of the pronotum and of certain mesothoracic sclerites and sulci. The shape of the pronotum as seen from above (Figure 28–9A–D) separates some families of sawflies, and its shape as seen from the side separates groups of superfamilies of Apocrita. The pronotum in the Apocrita may appear in profile more or less triangular and extending nearly or quite close to the tegulae (Figure 28–4C: Stephanoidea, Ceraphronoidea, Ichneumonoidea, Cynipoidea, Evanioidea, Proctotrupoidea, Platygastroidea, and some Vespoidea), somewhat quadrate and not quite reaching the tegulae (Figure 28–4A,B: Trigonalyoidea, Chrysidoidea, Chalci-

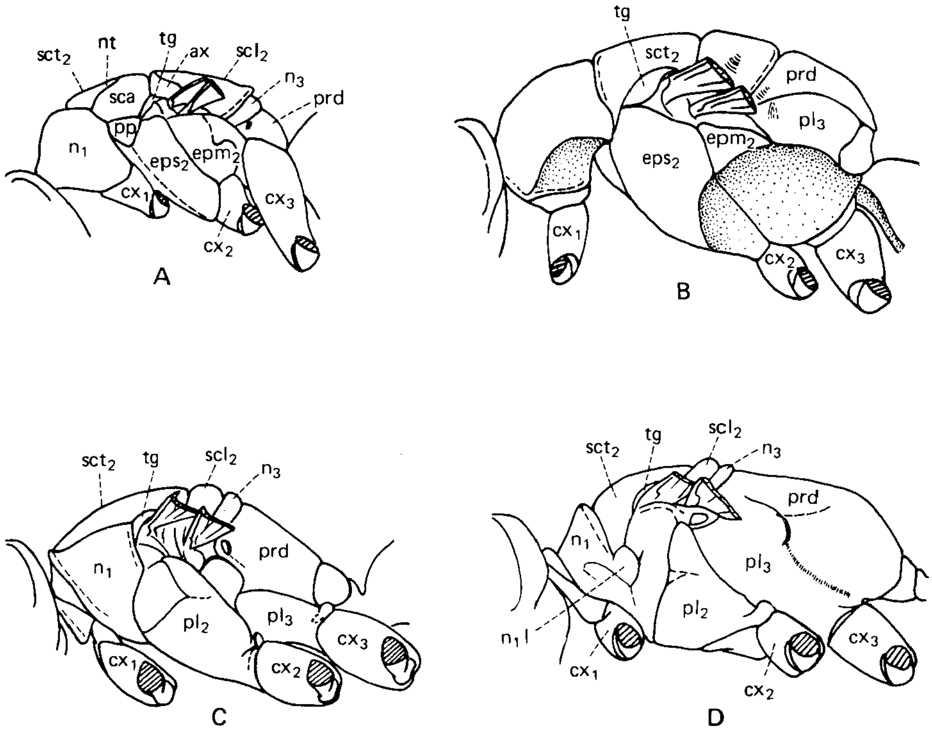

Figure 28–4 Mesosomatic structures in Hymenoptera, lateral view. A, chalcidoid (Torymidae); B, cuckoo wasp (Chrysididae); C, paper wasp (Vespidae); D, thread-waisted wasp (Sphecidae). *ax*, axilla; *cx*, coxa; *emp*, epimeron; *eps*, episternum; *n*, notum; n_1l, pronotal lobe; *nt*, notaulus; *pl*, pleuron; *pp*, prepectus; *prd*, propodeum; *sca*, scapula; *scl*, scutellum; *sct*, scutum; *tg*, tegula.

doidea, some Vespoidea), or short and collarlike with a small, rounded lobe on each side (Figures 28–4D and 28–12: Apoidea). Some Apocrita (for example, the Chalcidoidea) have a distinct triangular prepectus in the lateral wall of the mesothorax (Figure 28–4A, *pp*). The presence or absence of notauli (Figure 28–4A, *nt*, sometimes called *parapsidal furrows*) and the form of the axillae (Figure 28–4A, *ax*) often serve to separate related families. Most sawflies (all except Cephidae) have a pair of cenchri dorsally on or behind the metanotum. These are rounded and roughened structures that contact scaly patches on the posterior part of the fore wings and hold the wings in place when they are folded over the body (Figure 28–7, *cen*).

Abdominal Characters

In the superfamilies Ichneumonoidea, Stephanoidea, Cynipoidea, and Chalcidoidea, the ovipositor issues from the metasoma anterior to the apex, on the ventral side, and is not withdrawn into the body when not in use (Figure 28–5A). In most of the remaining Apocrita, the ovipositor issues from the apex of the metasoma and is withdrawn into the body when not in use (Figure 28–5B). The shape of the metasoma or of the petiole may separate related groups in some superfamilies.

Other Characters

In some wasps, the shape of the compound eyes differs in different families, with the inner or mesal margins sometimes strongly emarginate. The mouthpart structures used to separate groups of Hymenoptera are chiefly the form of the mandibles and the structure of the tongue (see Figure 28–6). The tongue provides some excellent characters for identifying bees and should be extended when specimens are fresh and still flexible. The head and thoracic characters that involve the form of sclerites and sulci are usually easy to see except when the specimen is very small or very hairy. In the latter case, it may be necessary to separate or remove the hairs. Characters such as the size, shape, or color of the insect provide easy means of identification in many groups. "Minute" means 2 mm long or less; small means 2–7 mm long.

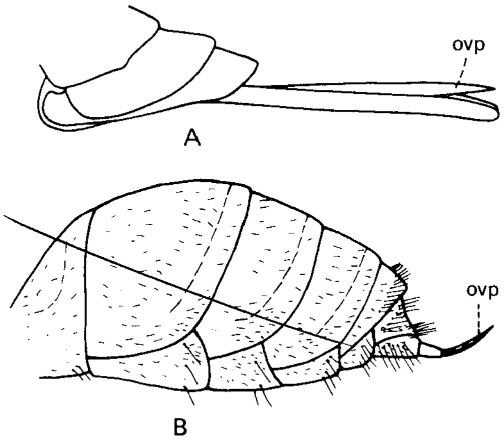

Figure 28–5 Position of the ovipositor in Hymenoptera. A, last sternite split ventrally, the ovipositor issuing from anterior to apex of abdomen (Ichneumonidae); **B**, last sternite not split ventrally, the ovipositor issuing from apex of abdomen (Sphecidae). *ovp*, ovipositor.

The principal difficulties likely to be encountered in keying out a specimen in this order are caused by the small size of some specimens. These are either difficult to see, or the specimens are weakly sclerotized and may collapse when air-dried. The larger specimens should not cause much difficulty. We have included here a key to all the families of Hymenoptera represented in the United States and Canada, although we realize the student is likely to have some difficulty in keying out the smaller specimens. Counts of the number of antennomeres and tarsomeres are best done by shining the light below the specimen so that the structure is seen in silhouette. Groups that are relatively rare or are small in size and unlikely to be found and retained by the beginning student are marked with an asterisk (*).

Key to the Families of Hymenoptera[2]

The system of venational terminology used by Richards (1977; Figure 28–1) is generally used in this key. Unless otherwise indicated, all venational characters refer to the front wing. For those species with highly reduced venation, the positional terms in Figure 28–19B are used. Cells are named according the the vein forming their anterior boundary; we continue to use the terms *submarginal* and *marginal cells*; cells used in the

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[2] We acknowledge here the generous and significant contributions to the chalcidoid portion of the key by G. A. P. Gibson, and to the bees by J. B. Whitfield.

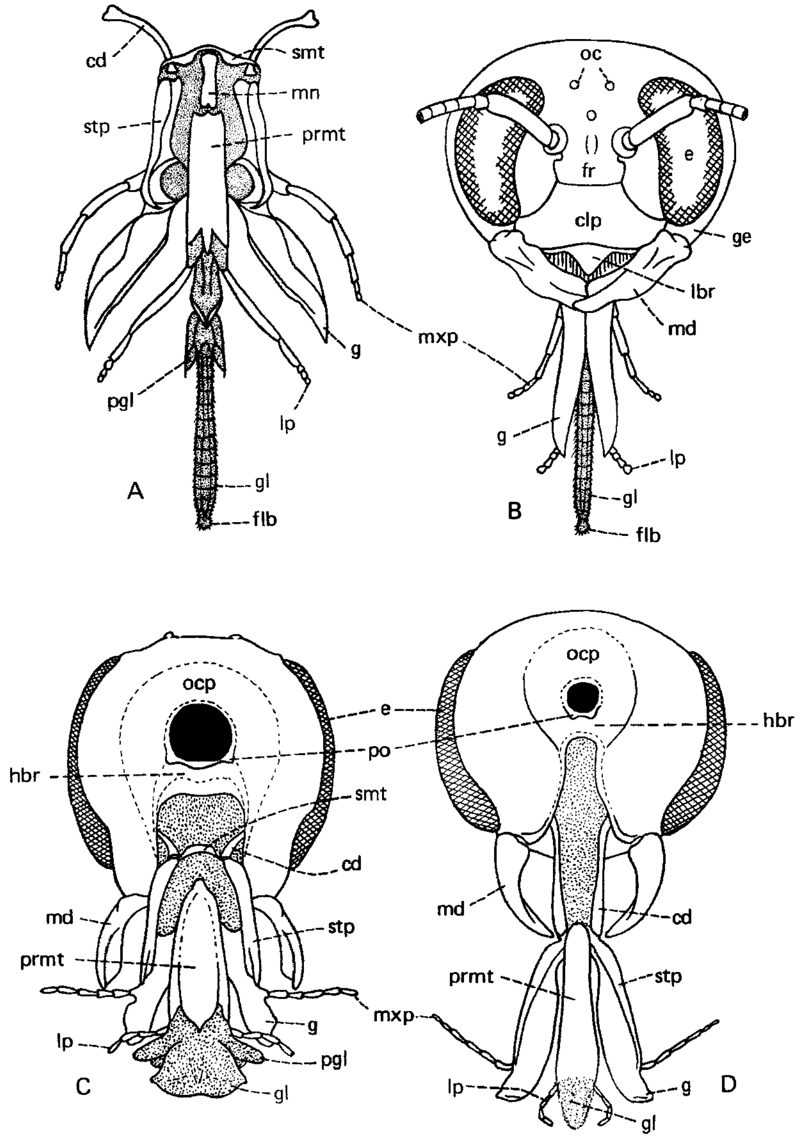
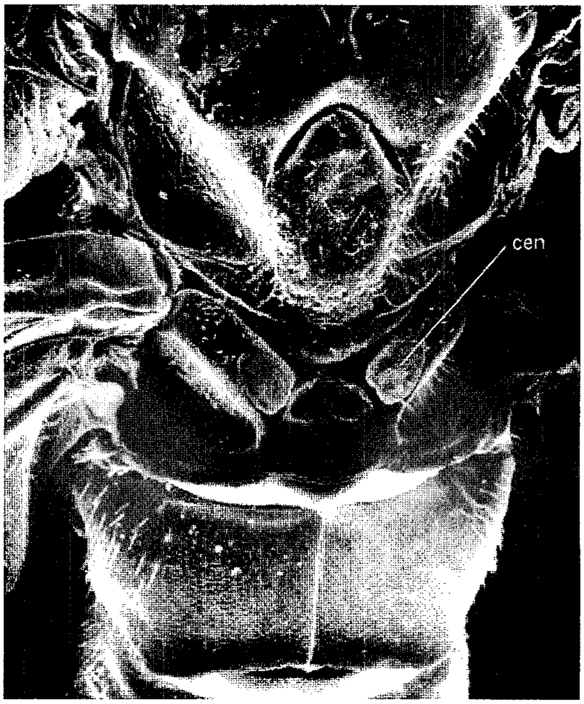


Figure 28–6 Head and mouthpart structure in bees. A, mouthparts of *Xylocopa* (Apidae, Xylocopinae), posterior view; B, same, anterior view; C, mouthparts of *Hylaeus* (Colletidae, Hylaeinae), posterior view; D, mouthparts of *Sphecodes* (Halictidae), posterior view. *cd*, cardo; *clp*, clypeus; *e*, compound eye; *flb*, flabellum; *fr*, frons; *g*, galea; *ge*, gena; *gl*, glossa; *hbr*, hypostomal bridge; *lbr*, labrum; *lp*, labial palp; *md*, mandible; *mn*, mentum; *mxp*, maxillary palp; *oc*, ocelli; *ocp*, occiput; *pgl*, paraglossa; *po*, postocciput; *prmt*, prementum; *smt*, submentum; *stp*, stipes.

key are labeled in the accompanying figures. The number of marginal or submarginal cells refers to the number of closed cells. No satisfactory keys to the family level or below are available that treat all Hymenoptera larvae, but Evans (1987) provides the most up-to-date keys for most groups. These are especially useful for sawfly larvae.

1. Base of abdomen broadly joined to thorax (Figures 28–7, 28–38 through 28–40), first abdominal tergum divided longitudinally (except Orussidae and rarely in Tenthredinidae), rarely these halves fused together, but fusion line visible; thorax with 2 pairs of spiracles, these located near wing bases and not visible dorsally; trochanters 2-segmented; hind wings nearly always with at least 3 closed basal cells (B in Figure 28–8); cenchri (Figure 28–7, *cen*) present (except Cephidae); body never shorter than 2 mm (sawflies) 2



Norman Johnson

Figure 28–7 Thorax and abdomen of Symphyta, dorsal view. *cen*, cenchri.

1′.	Base of apparent abdomen (the metasoma) constricted, more or less petiolate; first true abdominal tergum incorporated into functional thorax (the mesosoma), this therefore with 3 pairs of spiracles, the posterior pair clearly visible dorsally; trochanters 1- or 2-segmented; hind wings with 2 or fewer closed basal cells (Figures 28–2, 28–13, 28–14, 28–19, 28–20, 28–31, 28–36A–C); cenchri absent; rarely metasoma broadly connected to mesosoma in minute species (suborder Apocrita)	13	
2(1).	Antennae inserted under a broad frontal ridge below eyes, just above mouth (Figure 28–9E); 1 submarginal cell (Figure 28–8D)	Orussidae*	p. 519
2′.	Antennae inserted above base of eyes, near middle of face; 1–3 submarginal cells	3	
3(2′).	Front tibia with 1 apical spur	4	
3′.	Front tibia with 2 apical spurs	7	
4(3).	Pronotum in dorsal view wider than long, shorter along midline than laterally (Figure 28–9D); mesonotum with 2 diagonal furrows extending anterolaterally from anterior margin of scutellum (Figure 28–9D); abdomen terminating in a dorsally located, spearlike plate or spine	Siricidae	p. 518
4′.	Pronotum in dorsal view either U-shaped (Figure 28–9B) or more or less trapezoidal (Figure 28–9A,C); mesonotum without diagonal furrows; abdomen not terminating in a dorsally located spear or spine	5	
5(4′).	Pronotum in dorsal view U-shaped, posterior margin deeply curved, and very short along midline (Figure 28–9B); costal cell, and usually also vein Sc_2, present (Figure 28–8B); abdomen cylindrical	Xiphydriidae	p. 519

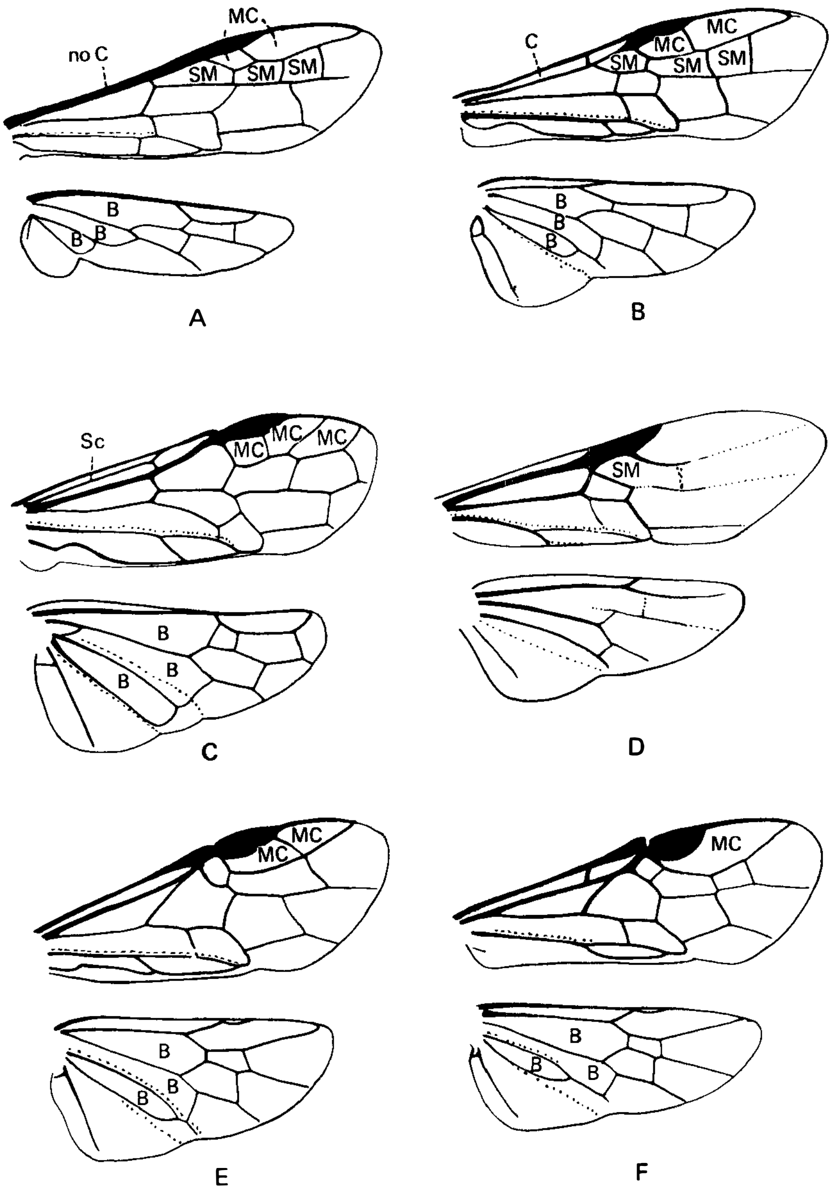


Figure 28–8 Wings of Symphyta. A, Cephidae (*Cephus*); B, Xiphydriidae (*Xiphydria*); C, Xyelidae (*Macroxyela*); D, Orussidae (*Orussus*); E, Tenthredinidae (*Dolerus*); F, Tenthredinidae (*Amauronematus*). *B*, basal cell; *C*, costal cell; *MC*, marginal cell; *sc*, subcostal vein; *SM*, submarginal cell.

5′.	Pronotum in dorsal view not U-shaped, posterior margin straight or only slightly curved (Figure 28–9A,C); costal cell present or absent; vein Sc_2 absent; abdomen more or less flattened laterally	6	
6(5′).	Costal cell present and distinct; apical spur on front tibiae pectinate on inner margin; pronotum in dorsal view much wider than long (Figure 28–9C); California and Oregon	Anaxyelidae*	p. 518
6′.	Costal cell absent or very narrow (Figure 28–8A); apical spur on front tibiae not pectinate on inner margin; pronotum in dorsal view about as long as or longer than wide (Figure 28–9A); widely distributed	Cephidae	p. 518
7(3′).	Antennae 3-segmented, third segment very long (Figure 28–10E), sometimes U-shaped	Argidae	p. 517

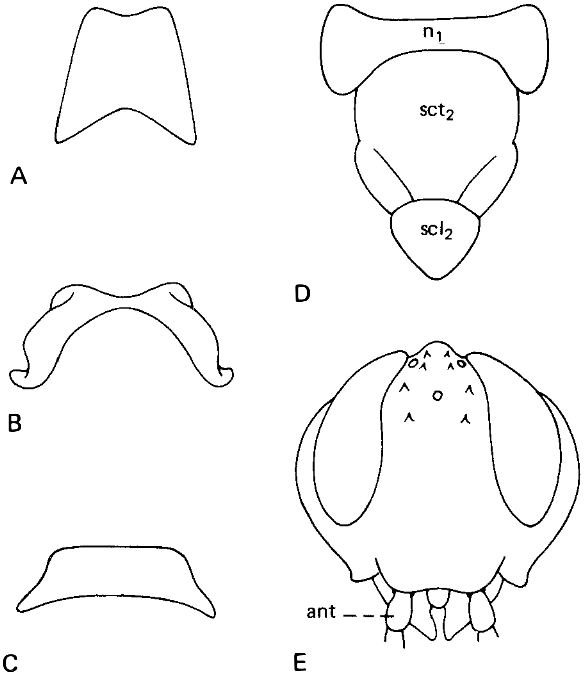


Figure 28–9 Head and thoracic characters of Symphyta. A–D, dorsal views; E, anterior view. A, pronotum of *Hartigia* (Cephidae); B, pronotum of *Xiphydria* (Xiphydriidae); C, pronotum of *Syntexis* (Anaxyelidae); D, thorax of *Urocerus* (Siricidae); E, head of *Orussus* (Orussidae). *ant*, base of antenna; n_1, pronotum; scl_2, mesoscutellum; sct_2, mesoscutum. (C, redrawn from Ross [1937]).

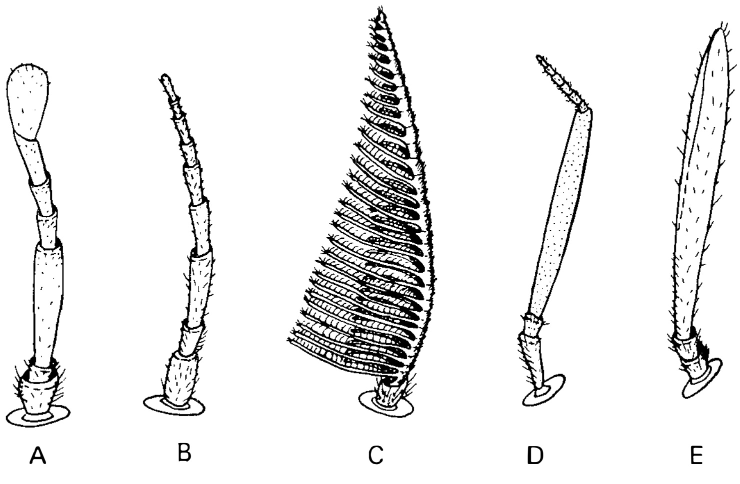


Figure 28–10 Antennae of Symphyta. A, Cimbicidae (*Cimbex*); B, Tenthredinidae (*Leucopelmonus*); C, male Diprionidae (*Neodiprion*); D, Xyelidae (*Macroxyela*); E, Argidae (*Arge*).

7′.	Antennae with more than 3 segments	8	
8(7′).	Third antennal segment very long, longer than following segments combined (Figure 28–10D); 3 (rarely 2) marginal cells and vein Sc present (Figure 28–8C)	Xyelidae*	p. 516
8′.	Third antennal segment short (Figure 28–10A–C); 1 or 2 marginal cells (Figure 28–8E,F); vein Sc usually absent	9	
9(8′).	Antennae clubbed, with 7 or fewer segments (Figure 28–10A); large, robust sawflies resembling bumble bees (Figure 28–38A)	Cimbicidae	p. 517

9′.	Antennae filiform (Figure 28–10B), serrate, or pectinate (Figure 28–10C), rarely slightly clubbed	10	
10(9′).	Antennae 6-segmented; anterior margin of scutellum more or less straight	Pergidae*	p. 516
10′.	Antennae with more than 6 segments; anterior margin of scutellum V-shaped (Figure 28–38B,C)	11	
11(10′).	Veins Sc and usually Cu_1 and crossvein cu-a present (Figure 28–1); antennae with 13 or more segments	**Pamphiliidae***	**p. 516**
11′.	Veins Sc and Cu_1 absent and crossvein cu-a present (Figure 28–8E,F); antennae variable	12	
12(11′).	Antennae 7- to 10-segmented and usually filiform (Figure 28–10B); 1 or 2 marginal cells (Figure 28–8E,F)	Tenthredinidae	p. 517
12′.	Antennae with 13 or more segments and either serrate or pectinate (Figure 28–10C); 1 marginal cell	Diprionidae	p. 517
13(1′).	First metasomatic segment (sometimes first 2 metasomatic segments) bearing a hump or node and strongly differentiated from rest of metasoma (Figures 28–11, 28–83); antennae usually elbowed, at least in female, with first segment long; pronotum more or less quadrate in lateral view, usually not reaching tegulae (Figures 28–11, 28–83); often wingless	Formicidae	p. 552
13′.	First metasomatic segment not as in preceding entry, or antennae not elbowed; pronotum variable	14	
14(13′).	Wings well developed	15	
14′.	Wings vestigial or lacking	106	
15(14).	Pronotum with a rounded lobe on each side posteriorly that does not reach the tegula (Figures 28–4D, 28–12); venation usually complete or nearly so (Figures 28–13, 28–14) (Apoidea)	16	

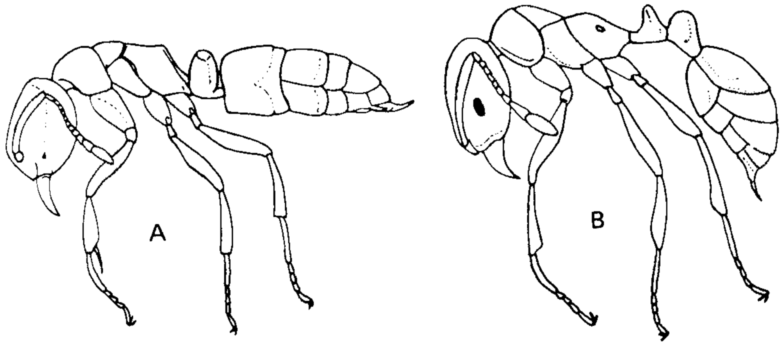


Figure 28–11 Ant workers. A, Ponerinae (*Ponera*); B, Myrmicinae (*Solenopsis*).

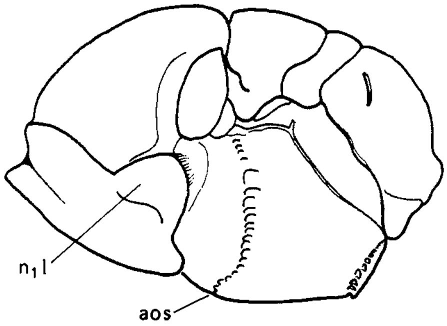


Figure 28–12 Mesosoma of *Hylaeus* (Colletidae, Hylaeinae); lateral view. *aos*, anterior oblique sulcus on mesepisternum; n_1l, pronotal lobe.

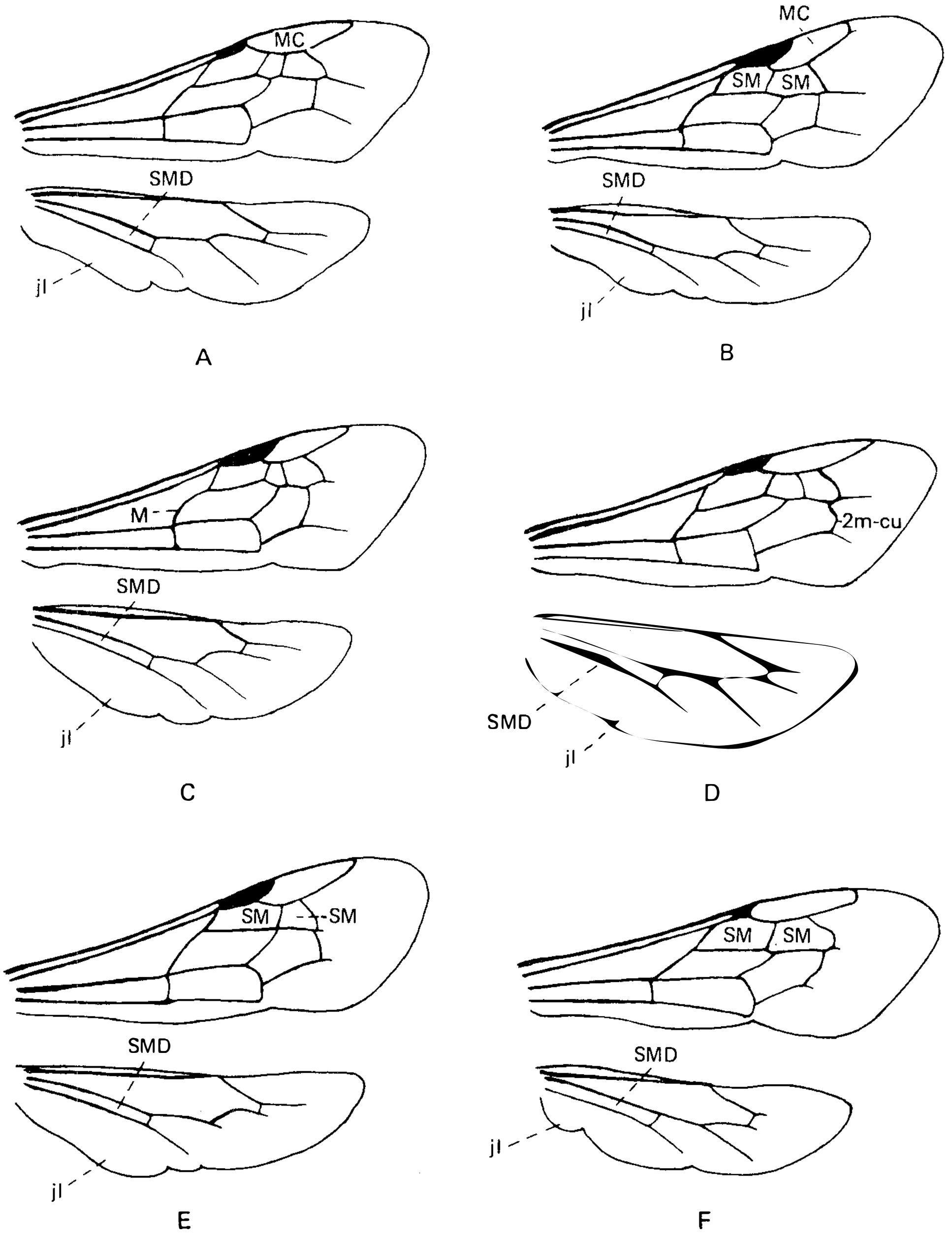


Figure 28–13 Wings of Apoidea. A, *Andrena* (Andrenidae, Andreninae); B, *Panurga* (Andrenidae, Panurginae); C, *Sphecodes* (Halictidae, Halictinae); D, *Colletes* (Colletidae, Colletinae); E, *Hylaeus* (Colletidae, Hylaeinae); F, *Coelioxys* (Megachilidae, Megachilinae). *jl*, jugal lobe; *MC*, marginal cell; *SM*, submarginal cells.

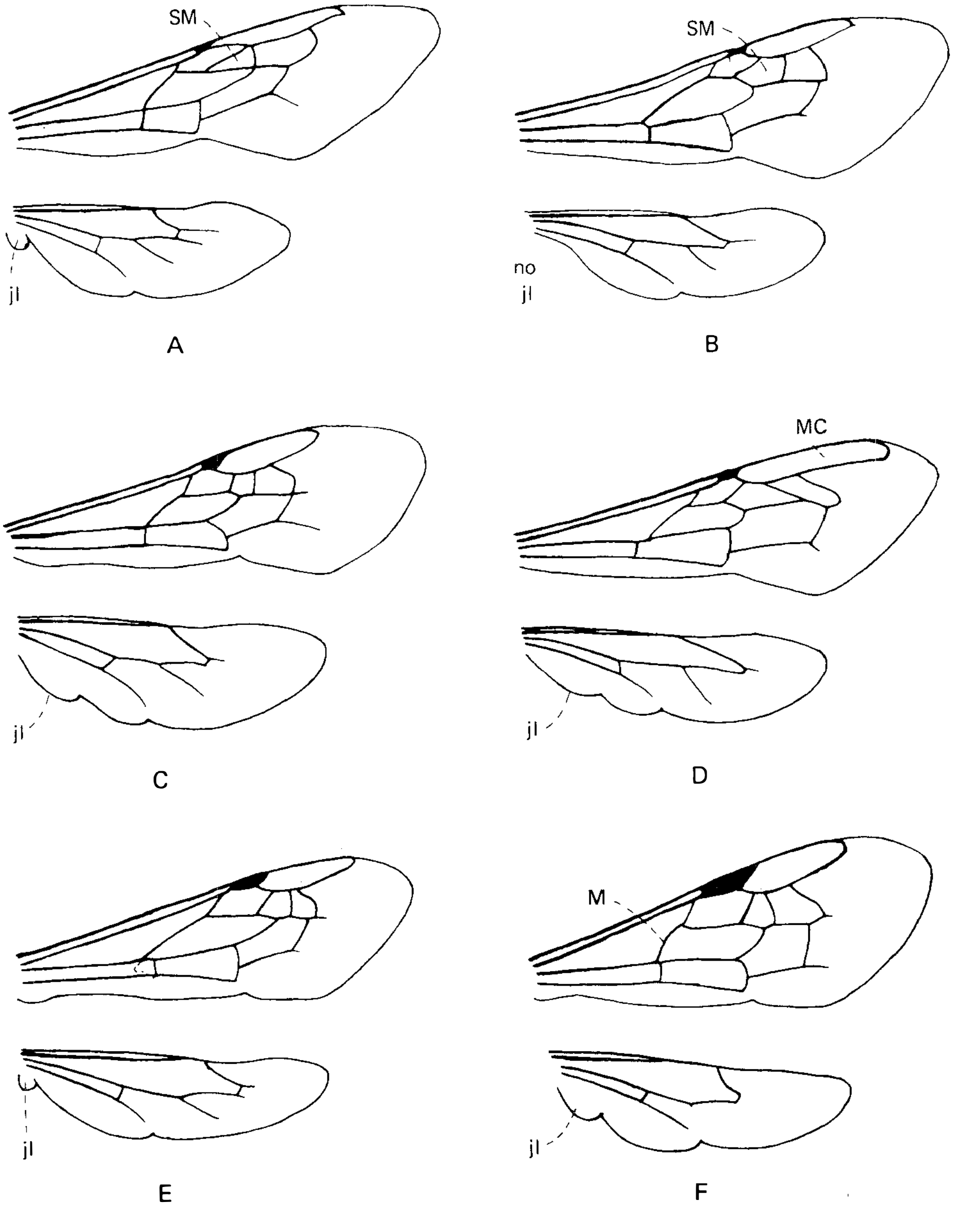


Figure 28–14 Wings of Apoidea. A, *Xylocopa* (Apidae, Xylocopinae); B, *Bombus* (Apidae, Apinae); C, *Melissodes* (Apidae, Apinae); D, *Apis* (Apidae, Apinae); E, *Nomada* (Apidae, Nomadinae); F, *Ceratina* (Apidae, Xylocopinae). *jl*, jugal lobe; *MC*, marginal cell; *SM*, second submarginal cell.

15′.	Pronotum without a rounded lobe on each side posteriorly (Figure 28–4A–C), or if such a lobe is present (as in Figure 28–34), it reaches (or nearly reaches) the tegula; venation variable, sometimes much reduced	22	
16(15).	Body relatively bare, with all body hairs unbranched; first segment of hind tarsus similar in width and thickness to the remaining segments and not longer than the remaining segments combined (Figure 28–15A); metasoma often petiolate; posterior margin of pronotum (in dorsal view) nearly always straight	Sphecidae	p. 539
16′.	Body usually relatively hairy, with at least some body hairs (especially on mesosoma) branched or plumose (Figure 28–16); first segment of hind tarsus usually wider than the remaining segments and generally as long as or longer than the remaining segments combined (Figure 28–15B–D); metasoma not petiolate; posterior margin of pronotum (in dorsal view) usually more or less arcuate	17	
17(16′).	Jugal lobe in hind wing as long as or longer than $M+Cu_1$ cell (Figure 28–13A–E, *jl*); galeae and glossa short	18	
17′.	Jugal lobe in hind wing shorter than $M+Cu_1$ cell or lacking (Figures 28–13F, 28–14); galeae and glossa usually long	20	
18(17).	Glossa truncate, bilobed apically (Figure 28–6C); anterior oblique sulcus present on mesepisternum (Figure 28–12, *aos*); frons with one subantennal sulcus meeting inner side of antennal socket (as in Figure 28–17C, *sas*)	Colletidae	p. 543
18′.	Glossa pointed or somewhat rounded apically, not bilobed (Figure 28–6A,B,D); anterior oblique sulcus often absent from mesepisternum; frons with one or two subantennal sulci	19	
19(18′).	Fore wing with first free segment of M strongly arched (Figure 28–13C); frons with 1 subantennal sulcus meeting inner side of antennal socket (as in Figure 28–17C); anterior oblique sulcus usually present on mesepisternum (as in Figure 28–12; *aos*); facial foveae absent	Halictidae	p. 543

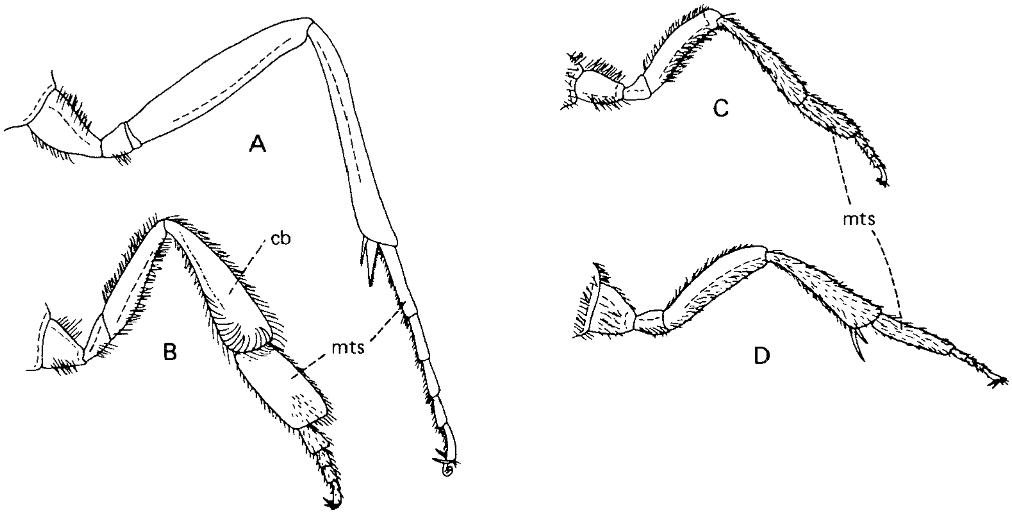


Figure 28–15 Hind legs of Sphecoidea (A) and Apoidea (B–D). A, *Sphex* (Sphecidae); B, *Apis* (Apidae); C, *Andrena* (Andrenidae); D, *Nomada* (Apidae). *cb*, corbicula; *mts*, first tarsal segment (metatarsus).

Norman Johnson

Figure 28–16 Scanning electron micrograph showing plumose body hairs of *Hylaeus* (Colletidae, Hylaeinae).

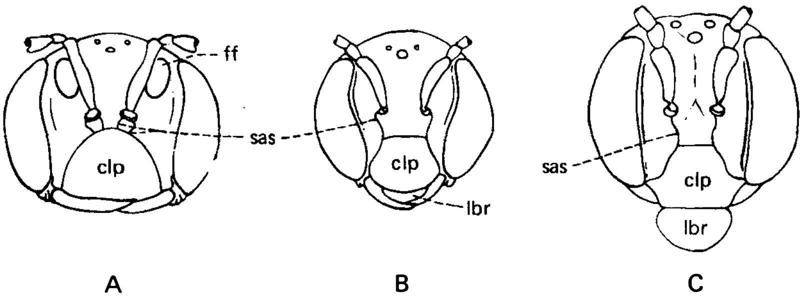


Figure 28–17 Heads of bees, anterior view. A, Andrenidae (*Andrena*); B, Megachilidae (*Osmia*); C, Apidae (*Doeringiella*, Nomadinae). *clp*, clypeus; *ff*, facial fovea; *lbr*, labrum; *sas*, subantennal sulcus.

19′.	Fore wing with first free segment of M straight or weakly arched (Figure 28–13A,B,D–F); frons with 2 subantennal sulci, one on each side of antennal socket (Figure 28–17A); anterior oblique sulcus almost always absent from mesepisternum; facial foveae, at least in females, present and distinct, often lined with dense, feltlike pile (Figure 28–17A)	Andrenidae	p. 543
20(17′).	Galeae and glossa short ("tongue" relatively short); segments of labial palpi similar and cylindrical (as in Figure 28–6D)	Melittidae	p. 540
20′.	Galeae and glossa elongate ("tongue" long); first 2 segments of labial palpi elongate and somewhat flattened to form a sheath for the "tongue" (Figure 28–6A,B)	21	
21(20′).	Fore wing with 2 submarginal cells (Figure 28–13F); labrum longer than wide, but with broad articulation with clypeus; subantennal sulci meeting outer side of antennal sockets (Figure 28–17B); scopa, when present, on metasoma (Figure 28–69)	Megachilidae	p. 544

21′.	Fore wing with 3 submarginal cells (Figure 28–14A, B), rarely 2; if 2, then second submarginal cell much shorter than first; labrum usually wider than long or with narrow articulation with clypeus; subantennal sulci meeting inner sides of antennal sockets (Figure 28–17C); scopa, when present, usually on hind legs (rarely also on metasoma)	Apidae	p. **545**
22(15′).	Venation slightly to considerably reduced, front wings usually with 5 or fewer closed cells, and hind wings usually without closed cells (Figures 28–19, 28–20, 28–31G)	23	
22′.	Venation complete or nearly so, front wings usually with 6 or more closed cells and hind wings with at least 1 closed cell (Figures 28–31A–F,H, 28–33)	83	
23(22).	Pronotum in lateral view more or less triangular, and extending to tegulae or nearly so (Figure 28–4C); hind wings nearly always without a jugal lobe	24	
23′.	Pronotum in lateral view more or less quadrate, and not quite reaching tegulae (Figure 28–4A,B); forms with 3 or more closed cells in front wings usually have a jugal lobe in hind wings	46	
24(23).	Metasoma arising on propodeum between bases of hind coxae or only slightly above them (as in Figure 28–18A–C); antennae variable	25	
24′.	Metasoma arising on propodeum far above bases of hind coxae (Figure 28–18D–F); antennae 13- or 14-segmented	84	
25(24).	Fore wing with well-developed marginal cell and costal vein absent basally, without enlarged stigma (Figure 28–19A)	26	
25′.	Fore wing either without marginal cell (as in Figure 28–19B–E, 28–20A,E) or costal vein present basally (Figure 28–20B–D,F–H); stigma often present	33	

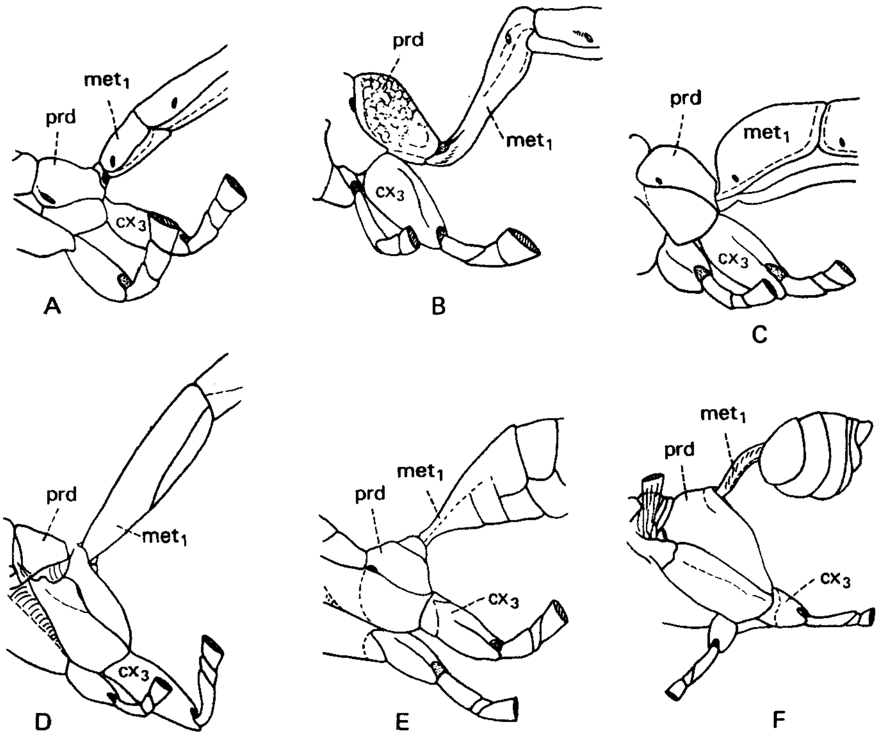


Figure 28–18 Base of the metasoma in parasitic Hymenoptera. A, Ichneumonidae; B, Ichneumonidae; C, Braconidae; D, Gasteruptiidae; E, Aulacidae; F, Evaniidae. *met*$_1$, first metasomatic segment; *cx*$_3$, hind coxa; *prd*, propodeum.

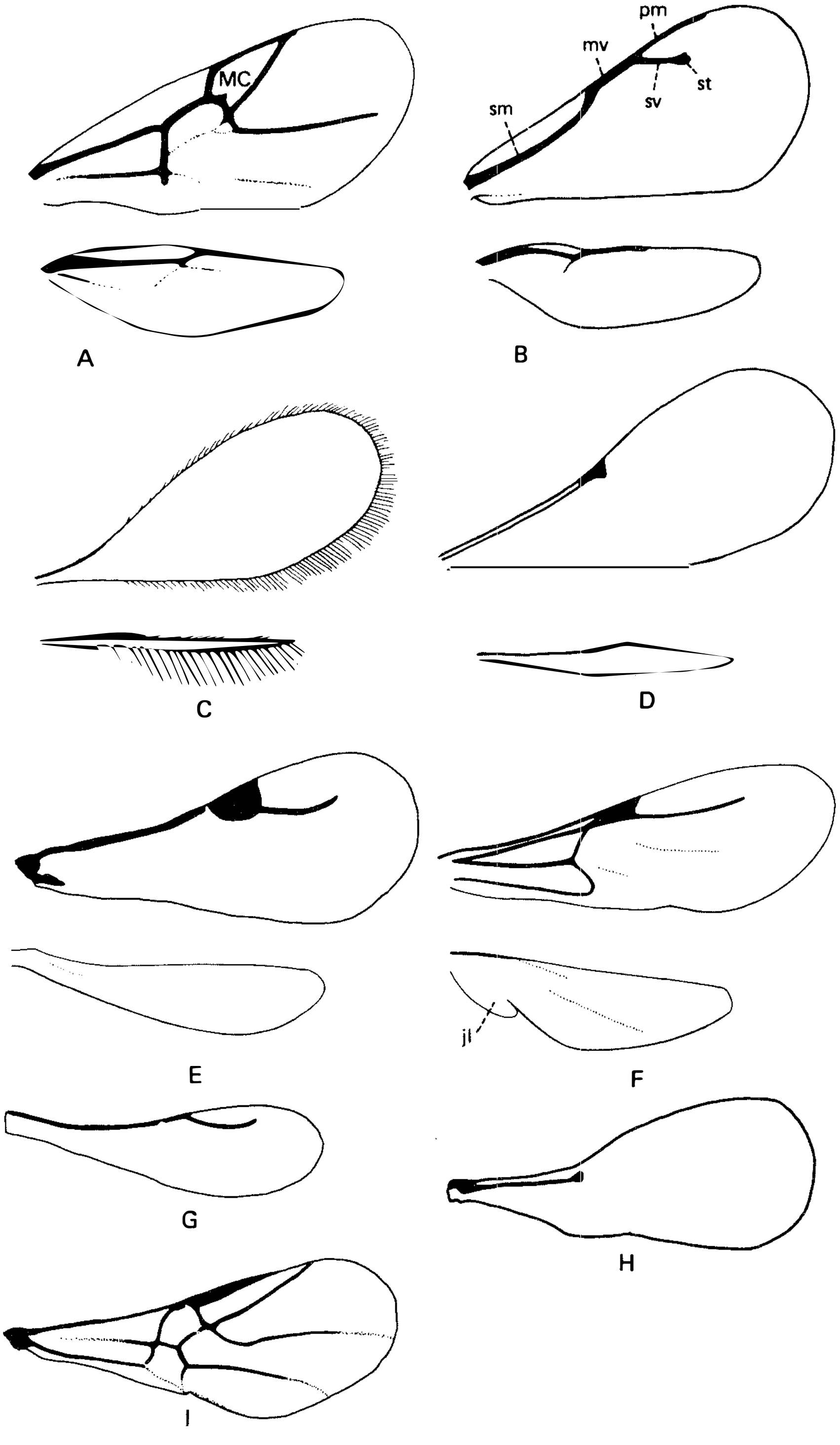


Figure 28–19 Wings of Hymenoptera. A, Cynipidae; B, Perilampidae; C, Mymaridae; D, Diapriidae (Diapriinae); E, Megaspilidae; F, Bethylidae; G, Ceraphronidae; H, Platygastridae; I, Ichneumonidae (Paxyllomatinae). *jl*, jugal lobe; *mv*, marginal vein; *pm*, postmarginal vein; *sm*, submarginal vein; *st*, stigma; *sv*, stigmal vein.

26(25).	First segment of hind tarsus twice as long as the other segments combined, second segment with a long process on outer side extending to tip of fourth segment (Figure 28–20B); metasoma compressed, longer than head and mesosoma combined; antennae 13-segmented in female and 15-segmented in male; 7–16 mm long	Ibaliidae*	p. 533
26′.	First segment of hind tarsi much shorter, the second segment without a long process on outer side; antennae variable, but usually 13-segmented in female and 14-segmented in male; generally 8 mm long or less	27	
27(26′).	In lateral view, tergum 4 or 5 of metasoma larger than other segments	Liopteridae	p. 534
27′.	In lateral view, tergum 2 or 3 of metasoma largest	28	
28(27′, 110).	Dorsal surface of scutellum with a rounded or oval elevation or keel in center (Figure 28–20D); first segment of Rs far longer than first free segment of M; second metasomatic tergum longer than third; antennae 11- to 16-segmented, usually 13-segmented in female and 15-segmented in male	Figitidae	p. 534
28′.	Dorsal surface of scutellum not as as in preceding entry; venation, metasomatic terga, and antennae variable	29	
29(27′).	Second metasomatic tergum narrow, tongue-shaped, shorter than third (Figure 28–20C); first segment of Rs far longer than first free segment of M	Figitidae*	p. 534
29′.	Second metasomatic tergum not tongue-shaped, or (some Cynipinae) tongue-shaped, but much longer than third	30	

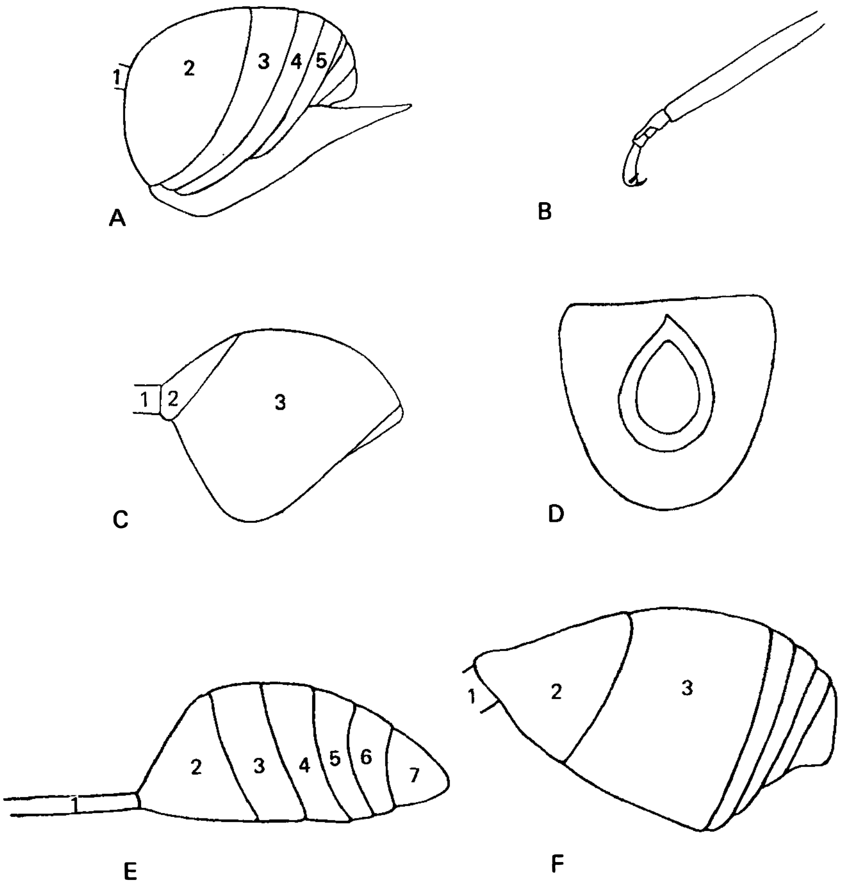


Figure 28–20 Characters of the Cynipoidea. A, metasoma of *Diplolepis* (Cynipidae); B, hind tarsus of *Ibalia* (Ibaliidae); C, metasoma of *Callaspida* (Figitidae); D, scutellum of Figitidae (Eucoilinae), dorsal view; E, metasoma of *Anacharis* (Anacharitinae); F, metasoma of Figitinae (Figitidae). The metasomatic tergites are numbered.

30(29′).	Petiole of metasoma elongate, in lateral view longer than wide; head distinctly wider than mesosoma	Figitidae	p. 534
30′.	Petiole short or hidden; head as wide as or narrower than mesosoma	31	
31(30′).	Pronotum dorsally with a differentiated medial plate; genal carina well-developed; scutellum sometimes prolonged in spine	Figitidae	p. 534
31′.	Upper surface of pronotum without separate medial plate; genal carina weak or absent; scutellum without posterior spine	32	
32(31′).	Head smooth; mid and hind tibia often with 1 apical spur; tarsal claw without basal tooth	Figitidae	p. 534
32′.	Head with coarse sculpture; mid and hind tibia with 2 apical spurs; tarsal claw often with basal tooth	Cynipidae	p. 534
33(25′).	Costal vein present in basal portion of fore wing and costal cell absent (Figure 28–19I, 28–21E)	34	
33′.	Either costal vein absent basally or costal cell well developed	35	
34(33).	Metasomatic tergites 2 and 3 fused together; Rs and M separated basad of 2r (Figure 28–21E)	Braconidae	p. 522
34′.	Metasomatic tergites 2 and 3 separated and overlapping; veins Rs and M not separating until beyond 2r (Figure 28–19I)	Ichneumonidae*	p. 523
35(33′, 110′).	Fore tibia with 2 apical spurs; venation highly reduced: no closed cells in fore wing, stigmal vein distinctly arched toward costal margin, marginal vein extending from base of wing, submarginal vein absent (Figure 28–19E,G) (veins rarely absent entirely) (Ceraphronoidea)	36	
35′.	Fore tibia with 1 apical spur; venation variable, submarginal vein usually present; in forms with reduced venation the stigmal vein, if present, either straight or curved away from costal margin	37	
36(35).	Middle tibia with 2 apical spurs; large apical spur on fore tibia forked apically; antennae 11-segmented in both sexes; stigma of fore wing usually large, semicircular (Figure 28–19E) (rarely linear or wings veinless in male Lagynodinae)	Megaspilidae	p. 520
36′.	Middle tibia with 1 apical spur; large spur of fore tibia not forked apically; female antennae 9- or 10-segmented, male antennae 10- or 11-segmented; stigma of fore wing linear, appearing similar to marginal vein, but separated from it by a distinct break (Figure 28–19G) (stigma and stigmal vein rarely absent)	Ceraphronidae	p. 520
37(35′, 90).	Antennal sockets separated from clypeal margin by distinctly more than 1 diameter of socket (Figure 28–22C, 28–59)	38	
37′.	Antennal sockets contiguous with dorsal margin of clypeus or separated from it by less than 1 diameter of socket (Figure 28–22A,B)	43	
38(37).	Antennae 10-segmented; hind wings with jugal lobe	Embolemidae*	p. 538
38′.	Antennae 11- to 16-segmented; hind wings without a jugal lobe (Figures 28–19D, 28–31G)	39	
39(38′).	Basitarsus of hind leg distinctly shorter than following segments; fore wing with Rs forked apically (Figure 28–21A)	Pelecinidae	p. 535
39′.	Basitarsus of hind leg distinctly longer than following segments; fore wing with Rs not forked or absent entirely	40	
40(39′).	First antennal segment distinctly elongate, at least 2.5 times as long as wide; antennae usually arising from a distinct shelf (Figure 28–59); stigma absent or very small (Figures 28–19D, 28–31G)	Diapriidae	p. 536
40′.	First antennal segment short, at most 2.2 times as long as wide; antennal shelf absent; stigma present (Figures 28–21D,F–H)	41	

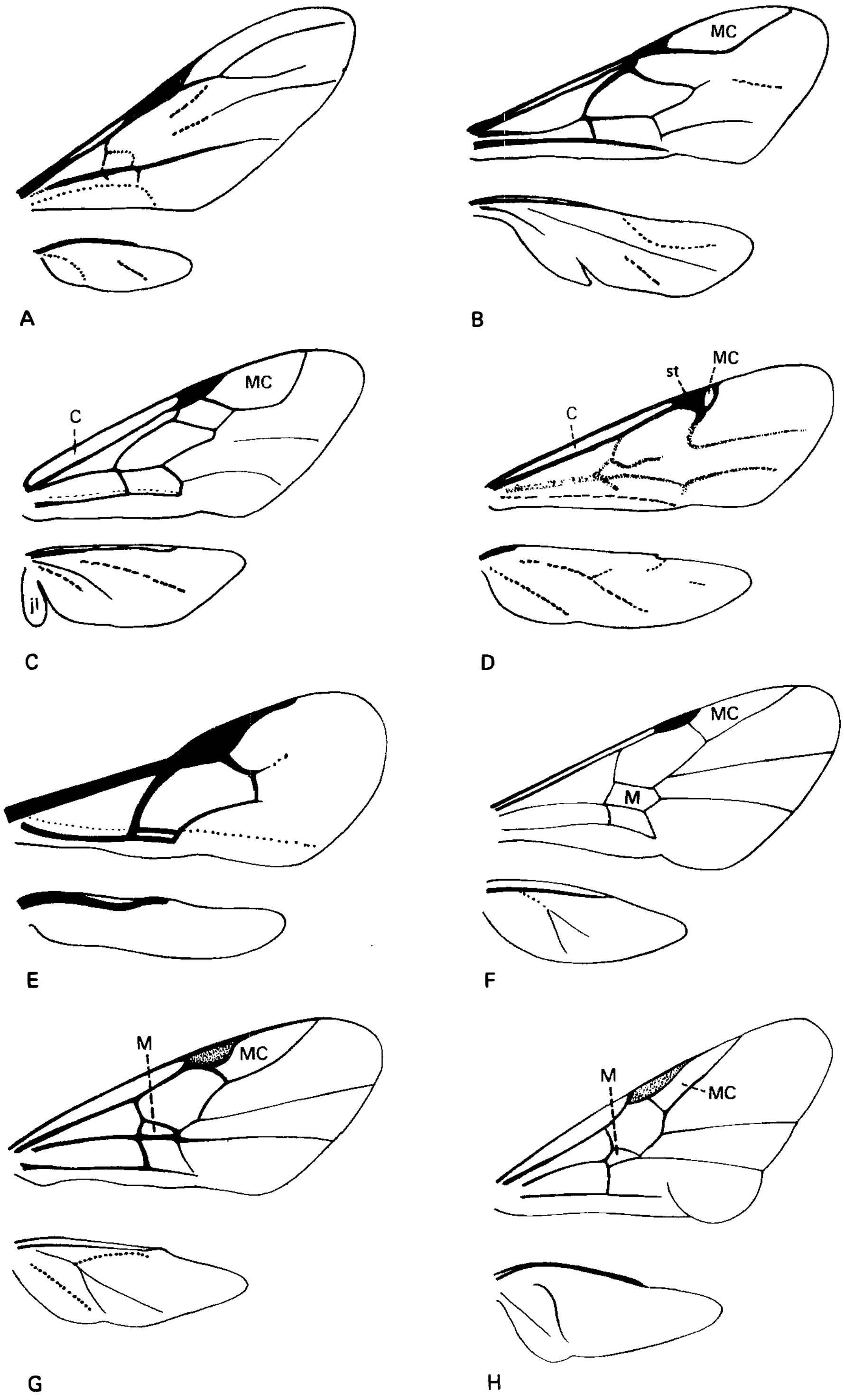


Figure 28–21 Wings of Hymenoptera. A, Pelecinidae; B, Chrysididae; C, Evaniidae; D, Proctotrupidae; E, Braconidae (Aphidiinae); F, Roproniidae; G, Vanhorniidae; H, Heloridae. *C*, costal cell; *jl*, jugal lobe; *M*, medial cell; *MC*, marginal cell; *st*, stigma.

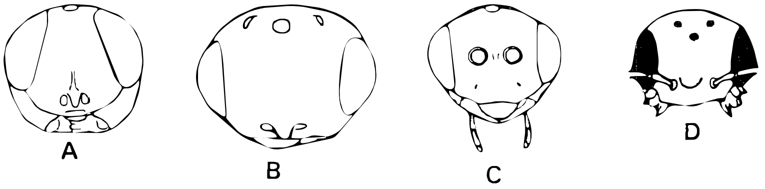


Figure 28–22 Head structure in the Platygastroidea and Proctotrupoidea, anterior view. A, Scelionidae; B, Platygastridae; C, Proctotrupidae; D, Vanhorniidae.

41(40′).	Antenna 13-segmented; medial cell not defined; marginal cell very narrow (Figure 28–21D)	Proctotrupidae	p. 536
41′.	Antenna with 14 or 16 segments; medial cell defined (Figure 28–21F,H, *M*); marginal cell elongate (Figure 28–21F,H)	42	
42(41′).	Antenna 16-segmented (including 1 minute ring segment following pedicel); metasoma slightly wider than high, in lateral view tergites subequal in height to sternites; medial cell triangular (Figure 28–21H, *M*)	Heloridae	p. 536
42′.	Antenna 14-segmented (without ring segment); metasoma strongly compressed laterally, in lateral view tergites much higher than sternites; medial cell polygonal (Figure 28–21F, *M*)	Roproniidae	p. 536
43(37′).	First antennal segment short and stout, less than 2 times as long as wide; antenna 13-segmented; mandibles with tips pointing outward, and widely separated when closed (Figure 28–22D); fore wing with thick stigma, marginal cell closed (Figure 28–21G)	Vanhorniidae	p. 535
43′.	First antennal segment long and slender, distinctly more than 2.5 times as long as wide; antenna never with 13-segments; mandibles normal, touching or crossing when closed; fore wing with stigma absent, marginal cell never closed	44	
44(43′).	Second metasomatic tergite distinctly longer than all others, several times longer than tergite 3	45	
44′.	Tergite 2 not distinctly longer than others, at most subequal in length to tergite 3	Scelionidae	p. 537
45(44).	Fore wing with stigmal and usually postmarginal veins; antennae usually 11- or 12-segmented, rarely 10-segmented	Scelionidae	p. 537
45′.	Fore wing without stigmal or postmarginal vein (Figure 28–19H), often entirely veinless; antenna with 10 or fewer segments	Platygastridae	p. 537
46(23′).	Venation greatly reduced (as in Figure 28–19B), the hind wings without an incision setting off a jugal or vannal lobe; antennae elbowed; mesosoma usually with a distinct prepectus (Figure 28–4A, pp); trochanters generally 2-segmented (Chalcidoidea)	47	
46′.	Wings with more veins, the hind wings usually with a lobe (jugal or vannal) set off by a distinct incision (Figures 28–19F, 28–21B); antennae usually not elbowed; trochanters usually 1-segmented (Chrysidoidea)	80	
47(46).	Hind femora greatly swollen and usually toothed or denticulate beneath (Figure 28–23E); hind tibiae usually arcuate	48	
47′.	Hind femora not swollen or only slightly swollen, and either not toothed beneath or with only 1 or 2 teeth	51	

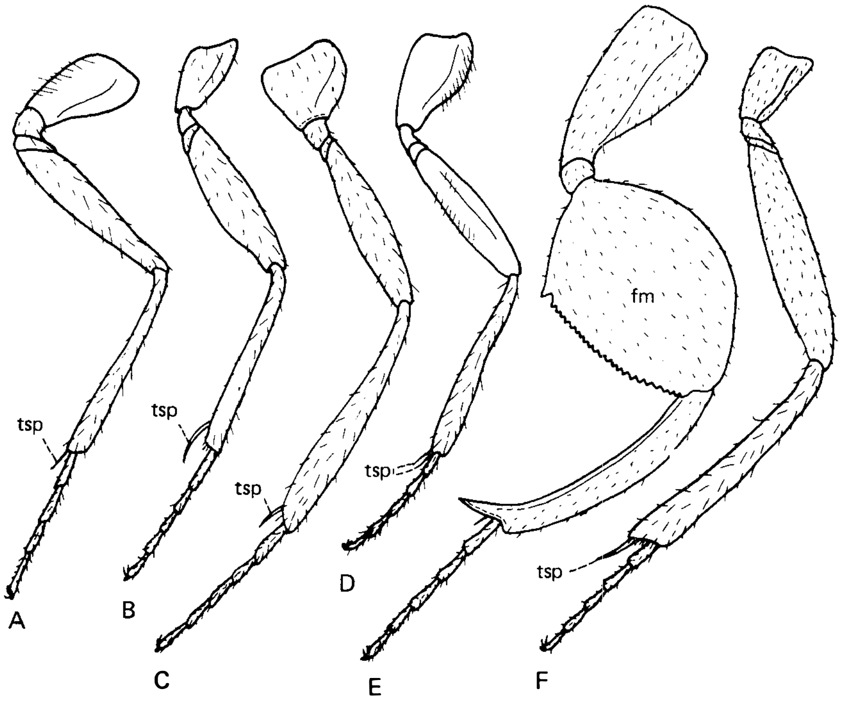


Figure 28–23 Legs of Chalcidoidea. A, front leg, Eulophidae; B, front leg, Pteromalidae; C, hind leg, Pteromalidae; D, hind leg, Eurytomidae; E, hind leg, Chalcididae; F, middle leg, Encyrtidae. *fm*, femur; *tsp*, tibial spur.

48(47).	Prepectus reduced and narrow, or almost entirely hidden; lateral angles of pronotum nearly reaching tegula; color black, brown, to yellow, never metallic	49	
48′.	Prepectus normal size, triangular, distinctly separating pronotum from tegula; color variable, often metallic	50	
49(48).	Fore wings usually folded longitudinally at rest; ovipositor curved up over dorsum of female; tegulae elongate	Leucospidae	p. 533
49′.	Fore wings not folded longitudinally; ovipositor directed posteriorly; tegula oval, not elongate	Chalcididae	p. 533
50(48′).	Inner margins of eyes diverging ventrally; antennae inserted distinctly below lower margins of eyes; body generally flattened	Pteromalidae	p. 532
50′.	Inner margins of eyes parallel; antennae inserted near to or distinctly above lower margins of eyes; body convex (Podagrioninae)	Torymidae	p. 532
51(47′, 112′).	Tarsi 3-segmented; wing pubescence often arranged in rows; minute insects	Trichogrammatidae	p. 530
51′.	Tarsi 4- or 5-segmented; wing pubescence usually not arranged in rows; size variable	52	
52(51′).	Petiole of metasoma 2-segmented, elongate; surface of fore wing with netlike reticulations; minute pale-colored species, less than 1 mm long	Mymarommatidae*	p. 526
52′.	Either metasomatic petiole 1-segmented or metasoma sessile; fore wing normal, usually setose, without reticulations; size and color variable	53	
53(52′).	Bases of antennae widely separated, inserted closer to eyes than to each other; frons with a distinct transverse sulcus above antennal insertions, and with a pair of longitudinal sulci along mesal margins of eyes (Figure 28–24); small to minute species, usually less than 1 mm long	Mymaridae	p. 526

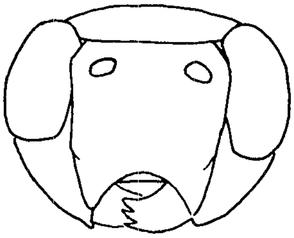


Figure 28–24 Head structure in Mymaridae.

53′.	Antennal insertions closer to each other than to eyes; frons without such sulci; size variable	54	
54(53′).	Tarsi 4-segmented	55	
54′.	Tarsi 5-segmented	60	
55(54).	Antennal funicle with 4 or fewer segments (Figure 28–25A,C)	56	
55′.	Antennal funicle with 5 or more segments (Figure 28–25B)	59	
56(55).	Hind coxa greatly enlarged and flattened; outer surface of hind tibiae with short, dark bristles arranged in zigzag lines or otherwise forming a distinctive pattern (Figure 28–26); fore wings narrow; male antennae branched	Eulophidae	p. 531

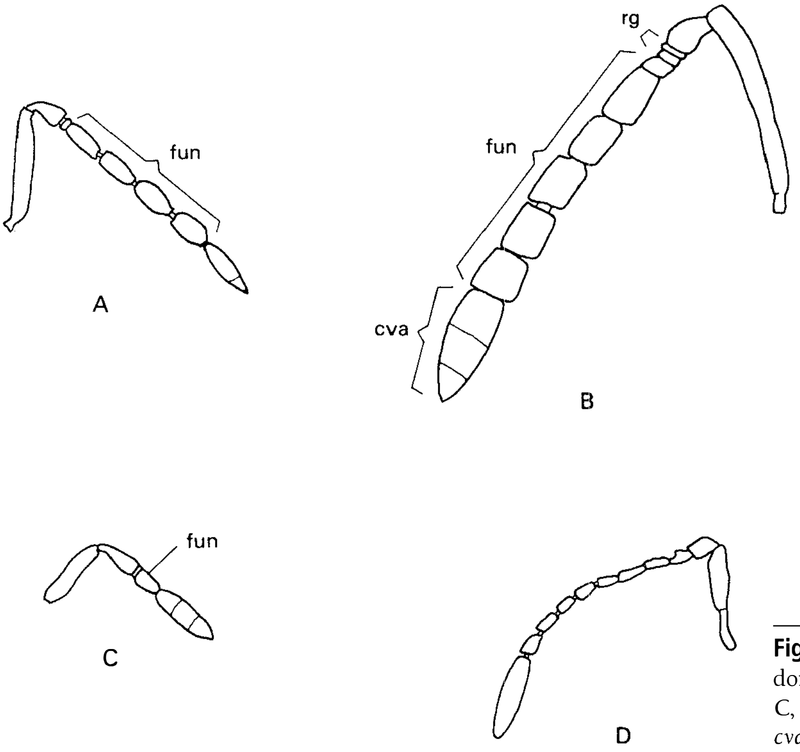


Figure 28–25 Antennae of Chalcidoidea. **A**, Eulophidae; **B**, Pteromalidae; **C**, Trichogrammatidae; **D**, Mymaridae. *cva*, clava; *fun*, funicle; *rg*, ring segments.

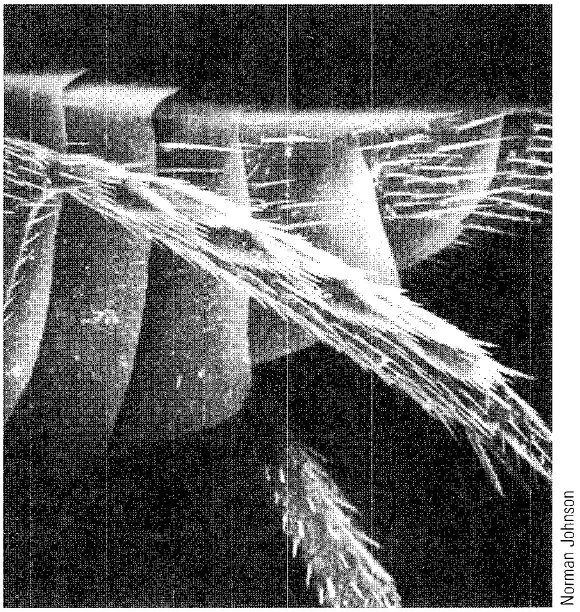


Figure 28–26 Hind tibia of *Elasmus* sp. (Eulophidae: Elasminae).

56′.	Hind coxa subequal in size to middle coxa; outer surface of hind tibia without bristles forming a pattern; fore wings and male antennae variable	57
57(56′).	Mesopleuron convex (as in Figure 28–27A); antennal clava long and unsegmented (and flagellum appearing to be 1-segmented) or body minute (<1 mm)	58

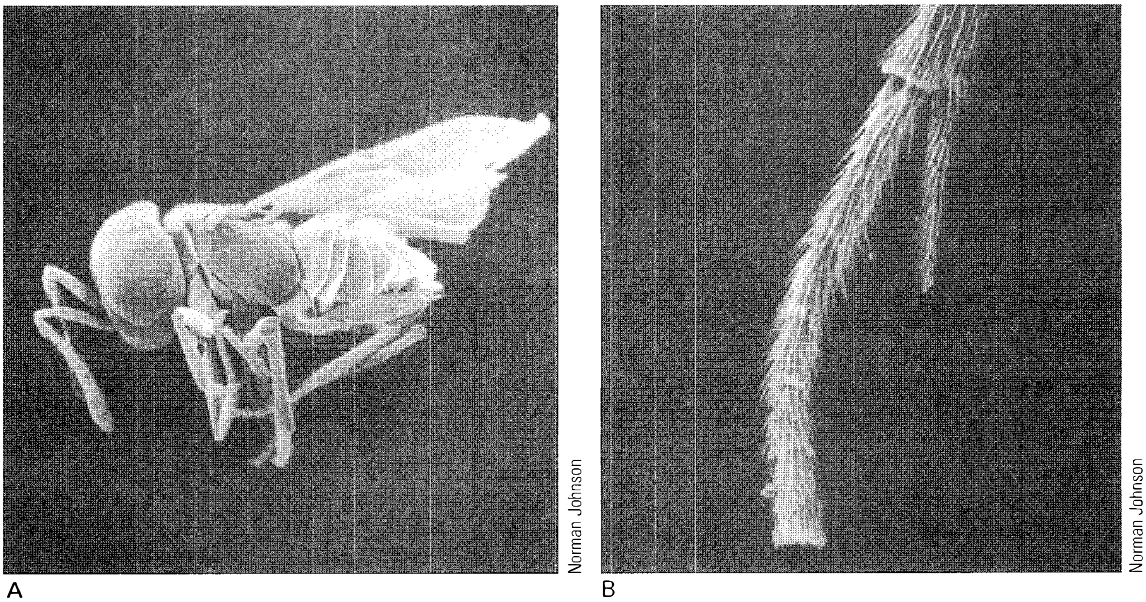


Figure 28–27 Encyrtidae. A, lateral habitus; B, tarsus and apex of tibia of middle leg.

57′.	Mesopleuron with well-developed groove for reception of middle femur; antennal clava usually short and divided into 2 or 3 segments; body rarely <1 mm	Eulophidae	p. 531
58(57).	Axillae meeting along dorsal midline of mesothorax; notauli absent; small, but >1 mm long	Encyrtidae*	p. 531
58′.	Axillae separated medially; notauli present; minute (<1 mm)	Aphelinidae*	p. 531
59(55′).	Notauli usually absent; mesopleuron convex (Figure 28–27A); midtibial spur long, thick (Figure 28–27B); middle basitarsal segment usually densely setose beneath; males and females; large, very common group	Encyrtidae	p. 531
59′.	Notauli complete; mesopleuron with groove for reception of middle femur; midtibial spur short, thin; basitarsus "normal"; males only	Tetracampidae*	p. 531
60(54′).	Head long, oblong, with a deep longitudinal groove above (Figure 28–52A); front and hind legs stout, tibiae much shorter than femora, middle legs slender (females; Florida, California, Arizona)	Agaonidae*	p. 532
60′.	Head and legs not as as in preceding entry	61	
61(60′).	Antennal funicle with 4 or fewer segments	62	
61′.	Antennal funicle with 5 or more segments	64	
62(61).	Axillae not separated from scutellum, together forming a narrow transverse band across mesosoma; propodeum with a median triangular area; middle tibia with lateral spurs	Signiphoridae	p. 531
62′.	Axillae distinctly separated from scutellum; propodeum without a distinct triangular area; middle tibia with apical spurs only	63	
63(62′).	Axillae contiguous medially; notauli absent	Encyrtidae	p. 531
63′.	Axillae widely separated medially; notauli present	Aphelinidae	p. 531
64(61′).	Mesopleura large and convex, usually without a femoral groove (Figure 28–27A); apical spur of middle tibia generally very large and stout (Figure 28–27B)	65	
64′.	Mesopleura with a groove for reception of the femora (Figures 28–28D, 28–29); apical spur of middle tibia not enlarged	67	
65(64).	Middle coxae inserted in front of midline of length of mesopleuron and nearly contiguous with fore coxae; prepectus flat; axillae wider than long and meeting medially	Encyrtidae	p. 535
65′.	Middle coxae usually inserted distinctly behind midline of length of mesopleuron and widely separated from fore coxae; rarely with middle coxae inserted near midline of length of mesopleuron, in these cases prepectus strongly protuberant, covering posterior margin of mesopleuron; axillae either not meeting medially or longer than wide	66	
66(65′).	Prepectus inflated and covering posterior portion of pronotum (especially apparent viewed from below); mesosoma compact; Florida, California, Arizona	Tanaostigmatidae*	p. 531
66′.	Prepectus flat, not protruding over pronotum; mesosoma usually elongate; widely distributed	Eupelmidae	p. 531
67(64′).	Mandibles sickle-shaped, with 1 or 2 teeth on inner side; mesosoma strongly elevated (Figure 28–28D); axillae contiguous and sometimes forming a transverse band anterior to scutellum; scutellum sometimes large and produced posteriorly; metasoma compressed, the second segment very large	Eucharitidae*	p. 533
67′.	Mandibles stout, not sickle-shaped, and with 3 or 4 teeth at apex; mesosoma not elevated; axillae usually separated, and triangular; scutellum and metasoma variable in shape	68	

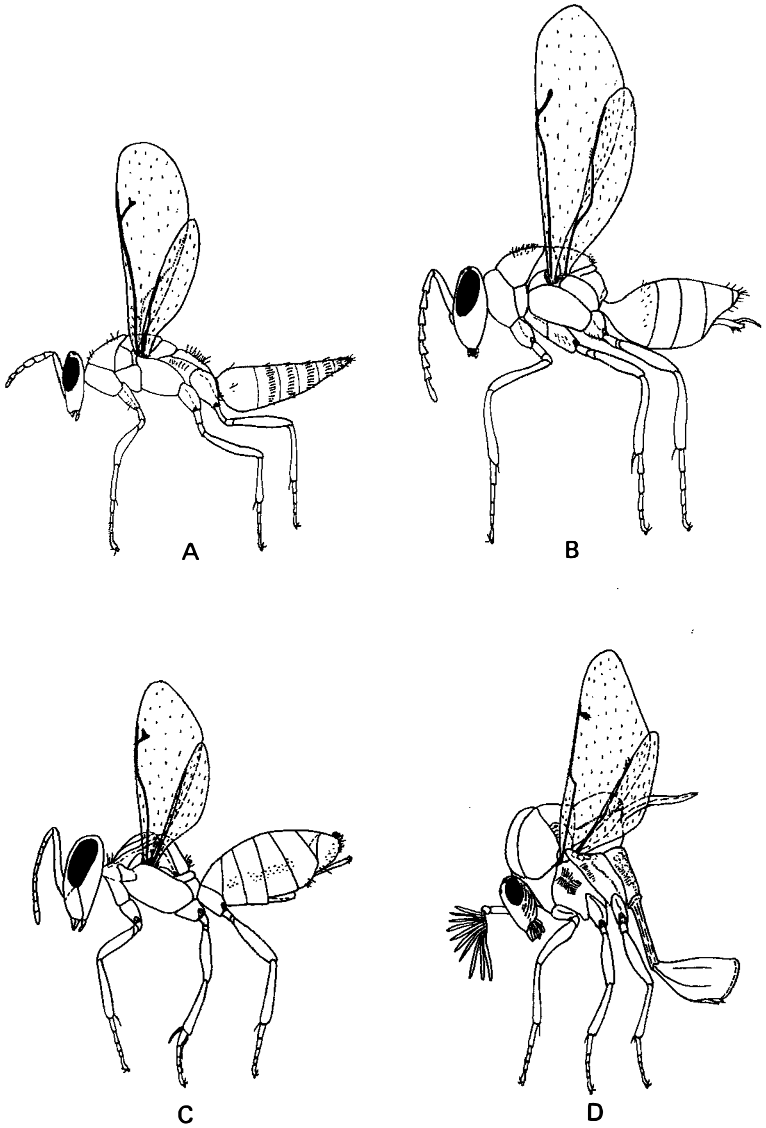


Figure 28–28 Chalcidoidea. A, Eulophidae; B, Encyrtidae; C, Eupelmidae; D, Eucharitidae.

68(67′). Metasoma dorsally with transverse rows of deep pits or with strongly developed transverse crenulae; metasoma of female conical and elongate, of male oblong; cerci short, sessile; hind tibia with 2 apical spurs, either with inner spur distinctly longer than outer and usually curved, or both very long **Ormyridae** p. 532

68′. Metasoma without such sculpture; hind tibiae with 1 or 2 spurs, these relatively straight and short, often difficult to see **69**

69(68′). Prepectus fused with pronotum or rigidly attached to it and anterior portion of mesepisternum; metasoma with petiole often very small and inconspicuous, first 2 large terga fused dorsally and covering at least half the metasoma, metasoma often appearing short and triangular in lateral view (Figure 28–29B); mesosoma usually coarsely punctate, robust **Perilampidae** p. 533

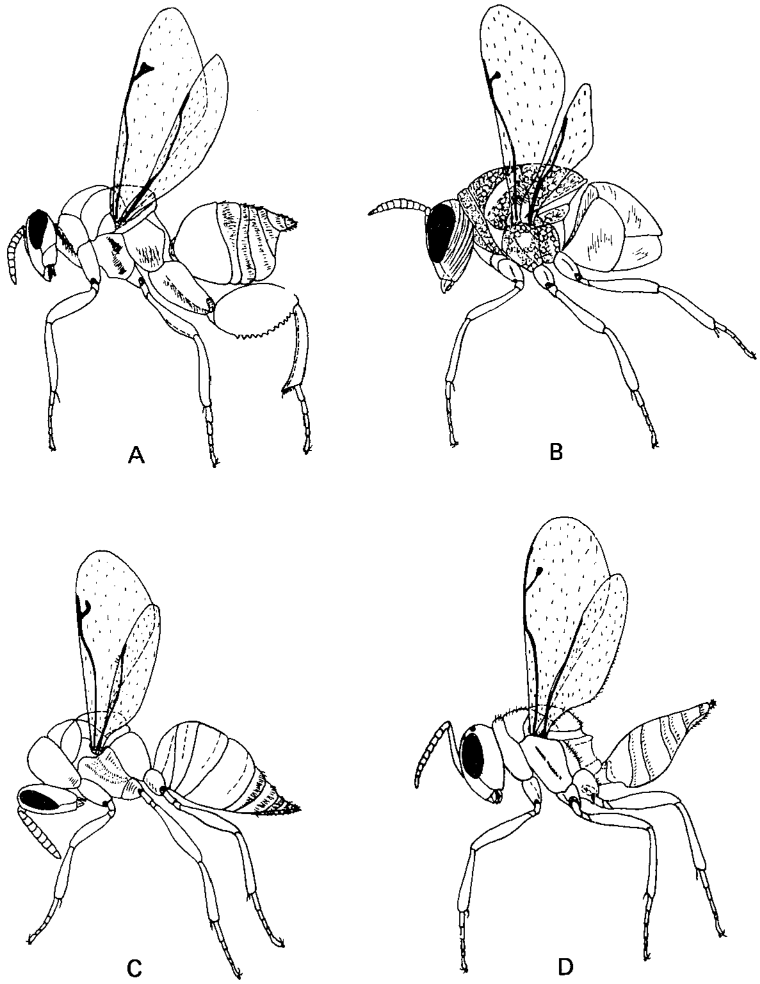


Figure 28–29 Chalcidoidea. A, Chalcididae; B, Perilampidae; C, Eurytomidae; D, Pteromalidae.

69′.	Prepectus present as an independent sclerite, not fused with pronotum; metasoma usually with terga 2 and 3 independent (except some Pteromalidae); mesosoma usually with fine sculpture dorsally, if coarsely punctate, then usually longer than high	70	
70(69′).	Females; metasoma either with ovipositor sheaths as long as or longer than mesosoma and metasoma combined, or metasoma with ovipositor sheaths and apical terga greatly elongated to form a distinctive "tail"	Torymidae	p. 532
70′.	Males and females; apical metasomatic terga not elongated, ovipositor sheaths distinctly shorter than combined length of mesosoma and metasoma	71	
71(70′).	Females; ovipositor sheaths at least one-third length of hind tibiae, often longer; cerci elongate, peglike; hind coxa much larger than fore coxae, more or less triangular in cross section	Torymidae	p. 532
71′.	Both males and females; ovipositor sheaths usually shorter; cerci very short, barely raised above surface of metasoma; hind coxa subequal in size to fore coxa, more or less circular in cross section	72	

72(71′).	Males; fore wing with postmarginal vein much shorter than marginal vein, subequal in length to stigmal vein; hind coxae much larger than fore coxae, more or less triangular in cross section; inner margins of eyes parallel in frontal view	Torymidae	p. 532
72′.	Males and females; fore wing venation not as as in preceding entry; hind coxae variable, if large and triangular in cross -section, then inner margins of eyes diverging ventrally	73	
73(72′).	Collar of pronotum (the posterior portion, excluding the narrowed, necklike anterior part) at least half as long as mesoscutum, elongate or rectangular in dorsal view	74	
73′.	Pronotal collar less than half length of mesoscutum, or pronotum with sides converging, bell-shaped	78	
74(73).	Stigma of fore wing with conspicuous knoblike expansion; funicle 7-segmented; prepectus large, triangular	Torymidae	p. 532
74′.	Stigma usually not greatly enlarged; if so, then funicle with 6 or fewer large segments and prepectus small and inconspicuous	75	
75(74′).	Head or body partly metallic in color	76	
75′.	Head and body entirely nonmetallic	77	
76(75).	Funicle 5-segmented; propodeum depressed or with longitudinal furrow medially	Eurytomidae	p. 533
76′.	Funicle with more than 5 segments or propodeum evenly convex or flattened	Pteromalidae	p. 532
77(75′).	Antennae inserted at or above lower margins of eyes; funicle usually with 6 or fewer segments, if with more then propodeum with longitudinal furrow medially	Eurytomidae	p. 533
77′.	Antennae inserted below lower margins of eyes; funicle either with 7 segments or propodeum flattened or convex, often with longitudinal carina medially	Pteromalidae	p. 532
78(73′).	Fore tibial spur short, straight, about one-fourth length of basitarsus; propodeum distinctly setose medially; pronotum as long as or longer than mesoscutum	Tetracampidae*	p. 531
78′.	Fore tibial spur usually distinctly curved, if not, then more than one-fourth length of basitarsus; propodeum bare; pronotum usually distinctly shorter than mesoscutum	79	
79(78′).	Males; apical spur of middle tibiae long, slender; apex of fore tibia with 1 or more short, stout spines on side opposite tibial spur; femoral groove on mesopleuron with minute, netlike sculpture; mesopleuron often with light line extending anteriorly from middle coxa	Eupelmidae	p. 531
79′.	Males and females; apical spur of middle tibia short and apex of fore tibia without spines; if otherwise, then femoral groove of mesopleuron with coarse, netlike sculpture or punctured and light lines absent	Pteromalidae	p. 532
80(46′).	Antennae with 22 or more segments and arising low on face; Arizona (males)	Sclerogibbidae*	p. 538
80′.	Antennae with 10–13 segments	81	
81(80′).	Antennae 10-segmented; front tarsi of female usually pincerlike (Figure 28–30)	Dryinidae*	p. 538
81′.	Antennae 12- or 13-segmented; front tarsi not pincerlike	82	
82(81′).	Metasoma with 3–5 visible terga, the last one often dentate apically; head not elongate; body usually metallic blue or green and coarsely sculptured	Chrysididae	p. 537

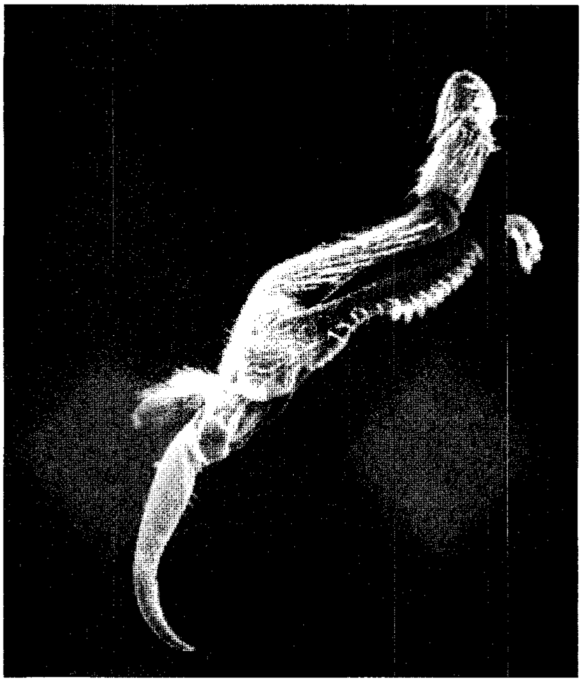


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Figure 28–30 Opened chela of fore leg of female dryinid.

82′.	Metasoma with 6 or 7 visible terga; head usually oblong and elongate; body black	Bethylidae	p. 537
83(22′).	Metasoma arising on propodeum far above bases of hind coxae (Figure 28–18D–F)	84	
83′.	Metasoma arising on propodeum between bases of hind coxae or only slightly above them (as in Figure 28–18A–C)	87	
84 (24′,83).	Hind wings with a distinct jugal lobe (Figure 28–20C); metasoma short, oval to circular and compressed, with a cylindrical petiole (Figure 28–18F, 28–43)	Evaniidae	p. 521
84′.	Hind wings without a distinct jugal lobe (Figure 28–31E,F); metasoma elongate	85	
85(84′).	Prothorax long and necklike; venation usually complete, the front wings with a stigma (Figure 28–31E,F); antennae 14-segmented; length over 8 mm; widely distributed	86	
85′.	Prothorax not long and necklike; venation reduced, much as in Figure 28–19A, the front wings without a stigma; antennae 13-segmented in female and 14-segmented in male; length less than 8 mm; Texas	Liopteridae	p. 534
86(85).	One m-cu crossvein or none, and 1 submarginal cell or none (Figure 28–31E); usually black, with relatively short antennae	Gasteruptiidae	p. 522
86′.	Two m-cu crossveins and 1 or 2 submarginal cells (Figure 28–31F); usually black with a reddish metasoma, and the antennae relatively long	Aulacidae	p. 522
87(83′).	Hind trochanters 2-segmented (Figure 28–32A), the distal segment sometimes poorly defined, rarely the trochanters 1-segmented; antennae with 14 or more segments; hind wings usually without a jugal lobe (Figure 28–31A–D); ovipositor variable, but sometimes long, half as long as metasoma or longer, and permanently exserted (Figure 28–5A)	88	

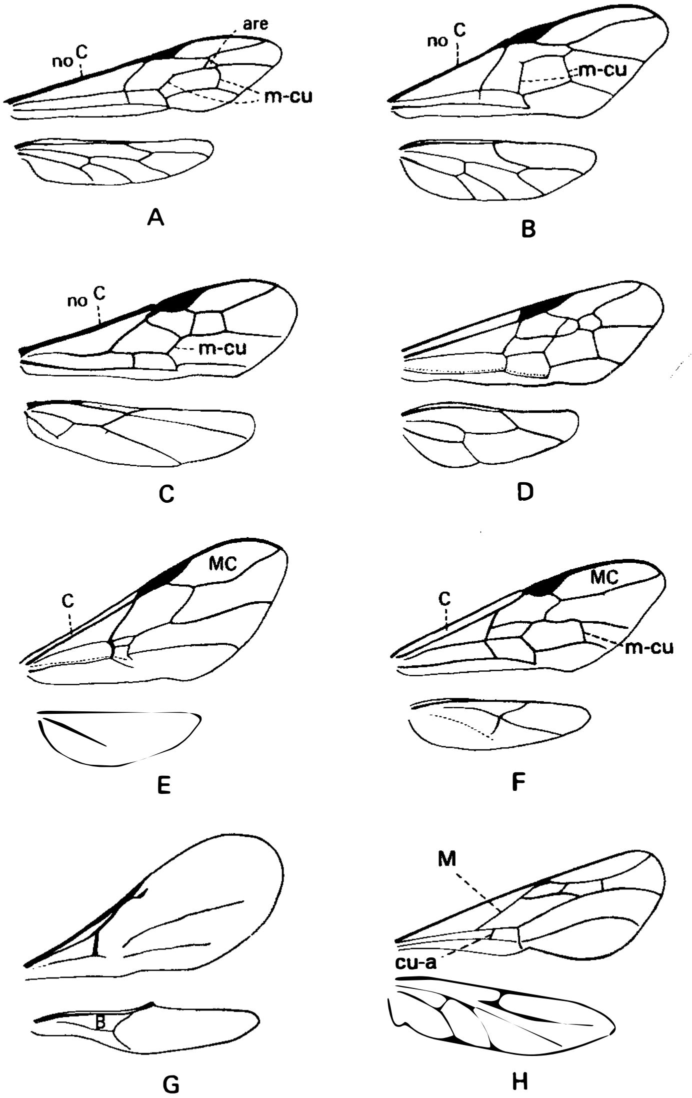

Figure 28–31 Wings of Hymenoptera. A, Ichneumonidae (*Megarhyssa*); B, Ichneumonidae (*Ophion*); C, Braconidae; D, Trigonalyidae; E, Gasteruptiidae; F, Aulacidae; G, Diapriidae (Belytinae); H, Rhopalosomatidae (*Rhopalosoma*). *are*, areolet; *B*, basal cell; *C*, costal cell; *MC*, marginal cell.

87′.	Hind trochanters 1-segmented (Figure 28–32B); antennae usually 12-segmented in females and 13-segmented in males; hind wings usually with a jugal lobe (Figure 28–33); ovipositor short, issuing from apex of metasoma (usually as a sting), and usually withdrawn into metasoma when not in use (Figure 28–5B)	92	
88(87).	Head somewhat spherical, set out on a long neck, and bearing a crown of teeth; costal cell usually present but narrow; 1 submarginal cell or none; female with a long ovipositor; length usually over 10 mm	Stephanidae*	p. 520
88′.	Head not as as in preceding entry; venation, size, and ovipositor variable	89	
89(88′).	Costal cell present (Figure 28–31D); ovipositor very short	90	
89′.	Costal cell absent (Figure 28–31A–C); ovipositor often long	91	
90(89).	Venation somewhat reduced, with not more than 1 submarginal cell; antennae 14- or 15-segmented	37*	

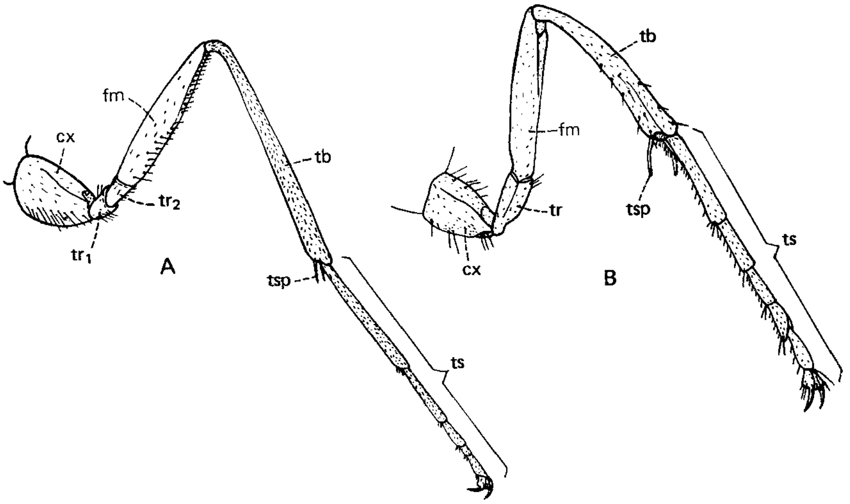

Figure 28–32 Legs of Hymenoptera. A, Ichneumonidae; B, Sphecidae. *cx*, coxa; *fm*, femur; *tb*, tibia; *tr*, trochanter; *ts*, tarsus; *tsp*, tibial spurs.

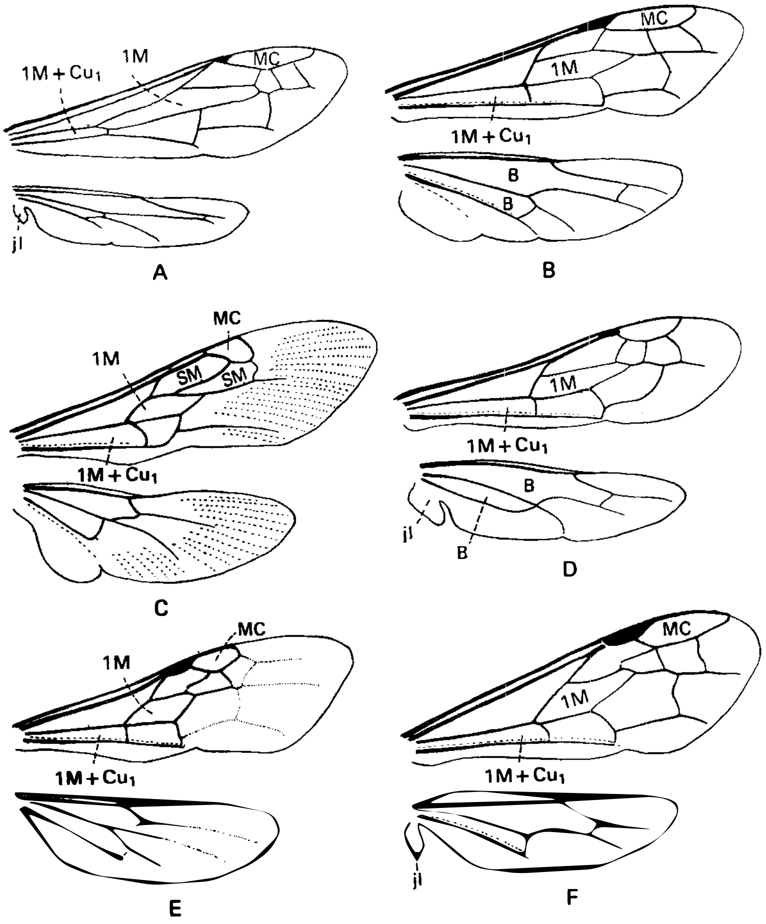

Figure 28–33 Wings of Hymenoptera. A, Vespidae (*Polistes*); B, Tiphiidae (*Myzinum*); C, Scoliidae (*Scolia*); D, Pompilidae; E, Mutillidae (*Dasymutilla*); F, Mutillidae (Myrmosinae). *B*, basal cell; *jl*, jugal lobe; *MC*, marginal cell; *SM*, submarginal cell.

90′.	Venation not reduced, with 2 or 3 submarginal cells; antennae with 16 or more segments	Trigonalyidae*	p. 521
91(89′).	Two m-cu crossveins (Figure 28–31A,B), or if with only 1, then the metasoma 3 times as long as rest of body and with tip of propodeum prolonged behind hind coxae; metasomatic tergites 2 and 3 independent, overlapping; vein Rs+M absent, first submarginal and 1M cells confluent; size variable, from a few millimeters up to 40 mm or more in length (excluding ovipositor)	Ichneumonidae	p. 523
91′.	One m-cu crossvein (Figure 28–31C) or none; first submarginal and 1M cells usually separated by vein Rs+M; metasoma not greatly elongate, tergites 2 and 3 (at least) fused; propodeum not prolonged behind hind coxae; mostly small insects, rarely over 15 mm long	Braconidae	p. 522
92(87′).	1M cell long, much longer than 1M+Cu_1 cell, and usually about half as long as wing (Figure 28–33A); wings usually folded lengthwise at rest; 3 submarginal cells; posterior margin of pronotum (in dorsal view) U-shaped	Vespidae	p. 549
92′.	1M cell usually shorter than 1M+Cu_1 cell and no more than one -third as long as wing (Figure 28–33B–F); wings usually not folded longitudinally at rest; 2 or 3 submarginal cells; posterior margin of pronotum (in dorsal view) usually straight or slightly arcuate	93	
93(92′).	Mesopleuron with a transverse sulcus (Figure 28–34, *su*); hind legs long, the hind femora usually extending to or beyond apex of metasoma; body bare	Pompilidae	p. 549
93′.	Mesopleuron without a transverse sulcus; legs shorter, the hind femora usually not extending to apex of metasoma; body often somewhat hairy	94	
94(93′).	Mesosternum and metasternum together forming a plate divided by a transverse sulcus, and overlapping bases of middle and hind coxae; the hind coxae well separated (Figure 28–35A); wing membrane beyond closed cells with fine longitudinal wrinkles (Figure 28–33C); apex of metasoma of male with 3 retractile spines; large, often brightly colored wasps	Scoliidae	p. 549

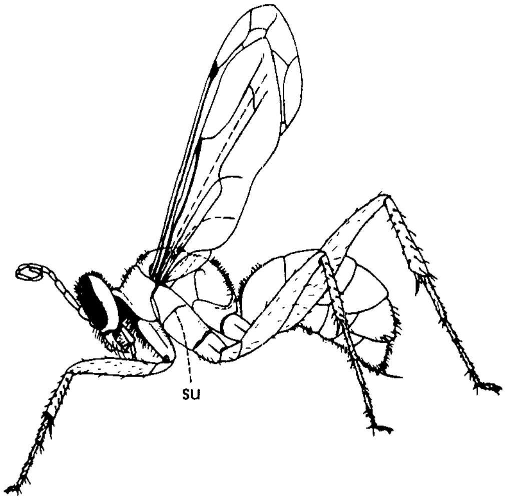

Figure 28–34 A spider wasp (Pompilidae), showing the transverse sulcus (*su*) across the mesopleuron.

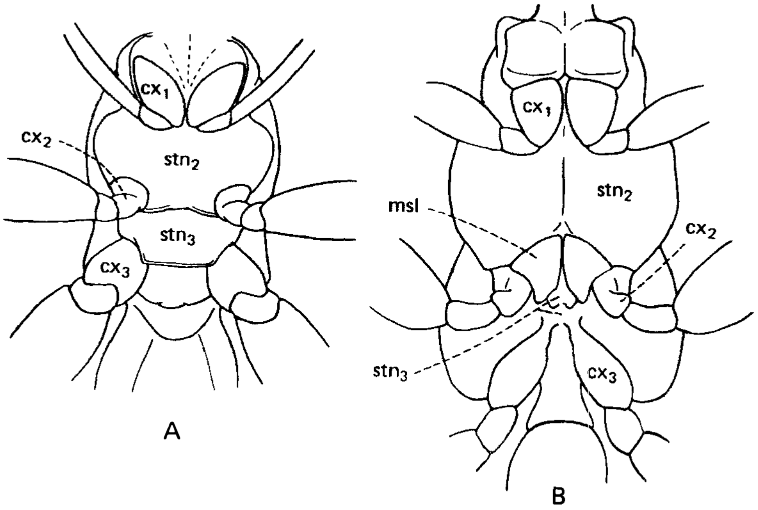

Figure 28–35 Mesosoma, ventral view. A, *Scolia* (Scoliidae); B, *Tiphia* (Tiphiidae). *cx*, coxa; *msl*, mesosternal lobe; *stn*$_2$, mesosternum; *stn*$_3$, metasternum.

94′.	Mesosternum and metasternum not forming such a plate, though there may be a pair of plates overlying bases of middle coxae (Figure 28–35B); hind coxae contiguous or nearly so; wing membrane beyond closed cells usually not wrinkled; apex of metasoma of male without 3 retractile spines; size and color variable	95	
95(94′).	Antennae clavate (Figure 28–36D); 2 submarginal cells (Figure 28–36A); length 10–20 mm; color usually black and yellow; western United States (Masarinae)	Vespidae	p. 549
95′.	Antennae not clavate; other characters variable	96	
96(95′).	Crossvein cu-a more than two-thirds its length distad of first free segment of M (between M+Cu$_1$ and Rs, Figure 28–31H); hind tarsi very long; flagellar segments of antennae long and slender, each with 2 apical spines; light brown wasps, 14–20 mm long	Rhopalosomatidae*	p. 549

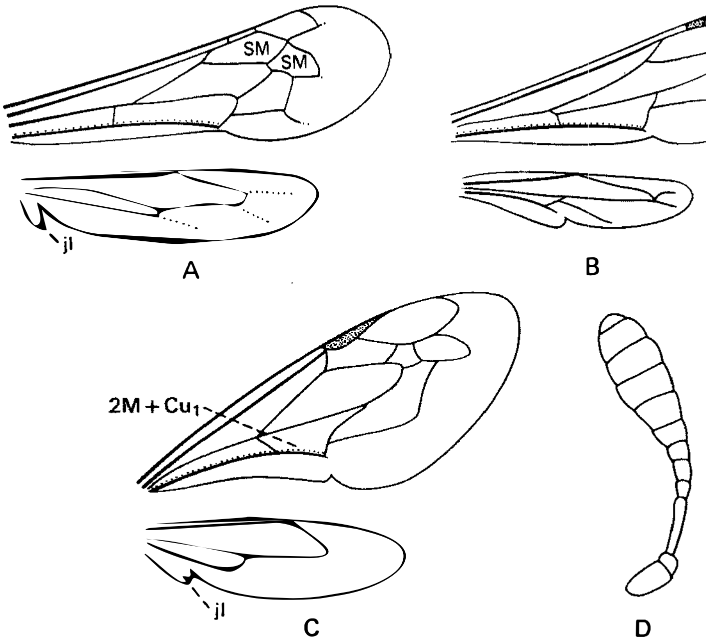

Figure 28–36 Characters of Vespidae. A, Wings of *Pseudomasaris* (Masarinae); B, wings of *Vespa* (Vespinae); C, wings of *Euparagia* (Euparagiinae); D, antenna of *Pseudomasaris* (Masarinae). *jl*, jugal lobe; *SM*, submarginal cell.

96′.	Crossvein cu-a opposite first free segment of M or nearly so (Figure 28–33E,F); tarsi not as in preceding entry; flagellar segments of antennae without apical spines; size and color variable	97	
97(96′).	Mesosternum with 2 lobelike extensions behind, which project between and partly cover bases of middle coxae (Figure 28–35B); hind wings with a jugal lobe (Figure 28–2) (Brachycistidinae, Tiphiinae, Myzininae, Anthoboscinae)	Tiphiidae	p. 547
97′.	Mesosternum without such lobes, at most a pair of minute toothlike projections behind; hind wings with or without a jugal lobe	98	
98(97′).	Apex of $2\mathrm{M}+\mathrm{Cu}_1$ cell produced above, and jugal lobe in hind wing about half as long as $1\mathrm{M}+\mathrm{Cu}_1$ cell (Figure 28–36C); length 6–7 mm; western United States (Euparagiinae)	Vespidae*	p. 549
98′.	Not exactly as in preceding description	99	
99(98′).	Hind wings with a distinct jugal lobe (Figure 28–33F)	100*	
99′.	Hind wings without a distinct jugal lobe (Figure 28–33E)	104	
100(99).	Metasomatic segments separated by strong constrictions; eyes usually not emarginate	101	
100′.	Metasoma without such constrictions; eyes sometimes emarginate	102*	
101(100).	Apex of abdomen with an upcurved spine; jugal lobe of hind wing at least half as long as cell $\mathrm{M}+\mathrm{Cu}_1$ (Methochinae)	Tiphiidae	p. 547
101′.	Apex of abdomen without an upcurved spine; jugal lobe in hind wing less than one-third as long as cell $\mathrm{M}+\mathrm{Cu}_1$ (Myrmosinae)	Mutillidae	p. 548
102(100′).	Body bare, marked with yellow or white; eyes deeply emarginate; widely distributed (Sapyginae)	Sapygidae*	p. 548
102′.	Body usually very hairy; color and eyes variable; western United States	103*	
103(102′).	Second metasomatic tergum with lateral submarginal felt lines (narrow longitudinal bands of relatively dense, closely appressed hairs); usually very pubescent (males)	Bradynobaenidae*	p. 549
103′.	Second metasomatic tergum without lateral felt lines; body and legs clothed with long, erect hairs; males and females (*Fedtschenkia*, California)	Sapygidae*	p. 548
104(99′).	Shining black, 4.5–6.0 mm long; second metasomatic tergum without lateral felt lines (see couplet 103); males without spines at apex of metasoma; eyes not emarginate mesally; males and females	Sierolomorphidae*	p. 548
104′.	Not shining black, but very hairy and often brightly colored; size variable but usually over 6 mm long; second metasomatic tergum usually with lateral submarginal felt lines; usually with 1 or 2 spines at apex of metasoma	105	
105(104′).	Middle tibia with 1 apical spur; antennal sockets not produced into tubercles (western United States)	Bradynobaenidae*	p. 549
105′.	Middle tibia with 2 apical spurs; antennal sockets produced dorsally into large tubercles (widespread)	Mutillidae	p. 548
106(14′).	Antennae with 16 or more segments	107	
106′.	Antennae with fewer than 16 segments	109	
107(106).	Hind trochanters 1-segmented (rarely 2-segmented); ovipositor issuing from apex of metasoma and usually withdrawn into metasoma when not in use; females; Arizona	Sclerogibbidae*	p. 538

107′.	Hind trochanters 2-segmented; ovipositor issuing from anterior to apex of metasoma and permanently exserted; widely distributed	108*	
108(107′).	Metasoma petiolate, petiole curved and expanded apically	Ichneumonidae*	p. 523
108′.	Metasoma not petiolate, or if petiolate, then petiole is not curved or expanded apically	Braconidae*	p. 522
109(106′).	Pronotum triangular in lateral view, reaching tegula posteriorly	110	
109′.	Pronotum more or less quadrate in lateral view, distinctly separated from tegula	111	
110(109).	Metasoma laterally compressed; ovipositor issuing from anterior to apex of metasoma and permanently exserted (wingless Cynipoidea)	28	
110′.	Metasoma cylindrical or depressed dorsoventrally, rarely laterally compressed; ovipositor issuing from apex of metasoma and usually withdrawn when not in use (wingless Embolemidae, Proctotrupoidea, Platygastroidea, Ceraphronoidea)	35	
111(109′).	First antennal segment elongate, antennae elbowed; prepectus well developed and triangular (Figure 28–4A, *pp*); ovipositor issuing from anterior to apex of metasoma and permanently exserted (wingless Chalcidoidea)	112	
111′.	Antennae filiform; ovipositor issuing from apex of metasoma, usually as a sting, and usually withdrawn into metasoma when not in use (Figure 28–5B)	114	
112(111).	Males; associated with figs; head prognathous, heavily sclerotized, often very large; ocelli absent	113	
112′.	Males and females; head hypognathous, of more normal size; ocelli present	51	
113(112).	Metasoma much drawn out to a point apically or broadened at tip; antennae short and stout, 3- to 9-segmented (see also couplet 60)	Agaonidae*	p. 532
113′.	Metasoma not pointed or enlarged apically	Torymidae*	p. 532
114(111′).	Second metasomatic segment with lateral felt lines (see couplet 103); body usually very pubescent; antennae usually 12-segmented, rarely 11- or 13-segmented; females	115	
114′.	Second metasomatic segment without lateral felt lines	116*	
115(114).	Pronotum immovably fused to mesoscuturn; lateral felt lines on tergum 2, sternum 2 or both; thoracic pleura flattened	Mutillidae	p. 548
115′.	Pronotum separated from rest of mesosoma by distinct, flexible articulation; lateral felt lines present only on tergum 2; thoracic pleura protuberant	Bradynobaenidae*	p. 549
116(114′).	Antennae 10-segmented	Dryinidae*	p. 538
116′.	Antennae 12- or 13-segmented	117*	
117(116′).	Antennae arising in middle of face; hind tarsi very long, nearly as long as tibiae and femora combined; first metasomatic segment long and slender; wings present but very short (*Olixon*)	Rhopalosomatidae*	p. 549
117′.	Antennae arising low on face, near margin of clypeus; tarsi and metasoma not as in preceding entry	118	
118(117′).	Head elongate, usually longer than wide; front femora usually thickened in middle; females	Bethylidae*	p. 537
118′.	Head not elongate, usually oval and wider than high	119	

119(118′).	Mesosternum with 2 lobelike extensions behind covering bases of middle coxae (Brachycistidinae)	**Tiphiidae**	p. 547
119′.	Mesosternum without such lobes, at most with a pair of minute, toothlike projections posteriorly	**120**	
120(119′).	Mesosoma divided into 3 parts (Methochinae)	**Tiphiidae**	p. 547
120′.	Mesosoma divided into 2 parts, the prothorax being well separated from the remaining fused segments (Myrmosinae)	**Mutillidae**	p. 548

The first 12 families in the following discussion are traditionally classified in the suborder Symphyta. Although this is clearly not a monophyletic group (the Apocrita are most closely related to the Orussidae), this taxon is still in wide use in the literature. We prefer to treat this group informally as either *symphytes* (lowercase) or *sawflies*.

Except for the family Orussidae, symphytes are phytophagous or xylophagous, and most are external feeders on foliage. The larvae of the external feeders are eruciform (Figure 28–37) and differ from the larvae of the Lepidoptera in having more than five pairs of prolegs that lack crochets and usually only one pair of stemmata. The larvae of a few species bore in stems, fruits, wood, or leaves (leaf miners). These larvae usually have reduced or absent prolegs. All symphytes have a well-developed ovipositor, used in inserting the eggs into the tissues of the host plant. In the Tenthredinoidea and Megalodontoidea, the ovipositor is somewhat sawlike, hence the common name "sawflies" for the members of this group.

Most sawflies have a single generation per year and overwinter as a full-grown larva or as a pupa, either in a cocoon or in some sort of protected place. Most external feeders overwinter in a cocoon or cell in the soil, whereas species that bore usually overwinter in their tunnels in the host plant. Some of the larger species may require more than one year to complete development.

Family **Xyelidae:** The Xyelidae are medium-sized to small sawflies, mostly shorter than 10 mm, that differ from other sawflies in having three marginal cells (Figure 28–8C) and the third antennal segment very long (longer than the remaining segments combined) (Figure 28–10D). Unlike all other sawflies except the Pamphiliidae, the costal cell of xyelids is divided by a longitudinal vein, the subcosta. The larvae feed on various trees. *Xyela* larvae feed on the staminate cones of pine; those of *Pleroneura* and *Xyelecia* bore in the buds and developing shoots of firs; and other species attack hickory and elm. In the early spring adults can be collected feeding on the catkins of willows and birches. This group is small (24 North American species), and none of its members is of very great economic importance.

Family **Pamphiliidae—Web-Spinning and Leaf-Rolling Sawflies:** These sawflies are stout-bodied and usually less than 15 mm long. About 75 species occur in North America. Some larvae are gregarious, and some feed singly. The gregarious ones live in silken nests formed by tying several leaves together, and the solitary ones live in a shelter formed by rolling up a leaf. Members of this group are uncommon, and only a few are of much economic importance. Some species of *Acantholyda* and *Cephalcia* are pests of conifers; *Neurotoma inconspicua* (Norton) (a web-spinning species) feeds on plum; and *Pamphilius persicum* MacGillivray (a leaf-rolling species) feeds on peach.

Family **Pergidae:** The sawflies in this group (4 North American species) are fairly small and occur from the eastern states west to Arizona, but are uncommon. Their larvae feed on the foliage of oak and

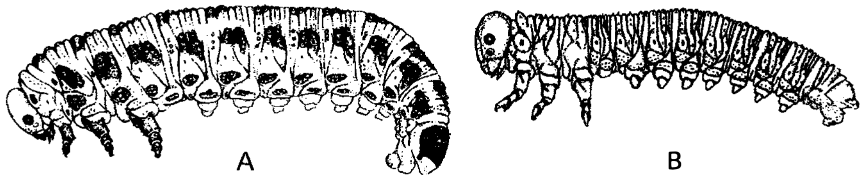

Figure 28–37 Sawfly larvae. A, *Neodiprion lecontei* (Fitch) (Diprionidae); B, *Allantus cinctus* (L.) (Tenthredinidae). (Courtesy of USDA.)

hickory. The North American species belong to the genus *Acordulecera*.

***Family* Argidae:** The Argidae are a small group (about 70 North American species) of medium-sized to small, stout-bodied sawflies, easily recognized by the characteristic antennae (Figure 28–10E). Males of a few species have the last antennal segment U-shaped or Y-shaped. Most argids are black or dark-colored. The larvae feed chiefly on various kinds of trees, but *Arge humeralis* (Beauvois) feeds on poison ivy, *Sphacophilus cellularis* (Say) feeds on sweet potato, and *Schizocerella pilicornis* (Holmgren) mines leaves of *Portulaca*.

***Family* Cimbicidae:** The Cimbicidae are large, robust sawflies with clubbed antennae. Only 12 species are found in the United States and Canada. Some resemble bumble bees. The most common species is the elm sawfly, *Cimbex americana* Leach, a dark blue insect 18–25 mm long (Figure 28–38A). The female has four yellow spots on each side of the abdomen. The full-grown larva of this species is about 40 mm long, with the diameter of a pencil, and is greenish yellow with black spiracles and a black stripe down the back. At rest or when disturbed, it assumes a spiral position. Often, when disturbed, it ejects a fluid, sometimes for a distance of several centimeters, from glands just above the spiracles. This species has one generation a year and overwinters as a full-grown larva in a cocoon in the ground. It pupates in the spring, and the adults appear in early summer. The larvae feed chiefly on elm and willow. Other species are commonly found feeding on honeysuckle.

***Family* Diprionidae—Conifer Sawflies:** These medium-sized sawflies have 13 or more antennal segments. The antennae are serrate in the female and pectinate or bipectinate in the male (Figures 28–10C, 28–38B,C). The larvae (Figure 28–37A) feed on conifers. They sometimes do serious damage, and species of *Diprion* and *Neodiprion* have been important forest pests, especially in Canada and the northern United States. Forty-five species occur in this area.

***Family* Tenthredinidae—Common Sawflies:** This is a very large group (about 800 North American species), and probably 9 out of 10 of the sawflies the general collector is likely to encounter will belong to this family. The adults are wasplike insects, often brightly colored, and are usually found on foliage or flowers searching for host plants, mates, or prey (many of the adults are predaceous). They are medium-sized to small, rarely over 20 mm long (Figure 28–39). The larvae (Figure 28–37B) are eruciform, and most are external feeders on foliage. When feeding, they usually have the

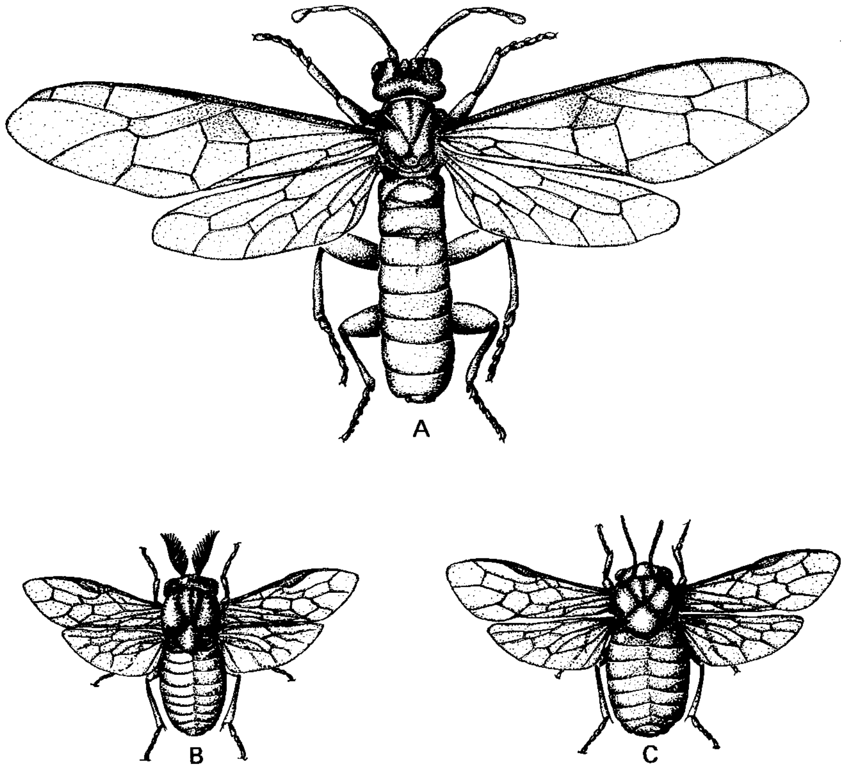

Figure 28–38 Sawflies. A, the elm sawfly, *Cimbex americana* Leach, male (Cimbicidae); B, the redheaded pine sawfly, *Neodiprion lecontei* (Fitch), male (Diprionidae); C, same, female. (B and C, redrawn from USDA.)

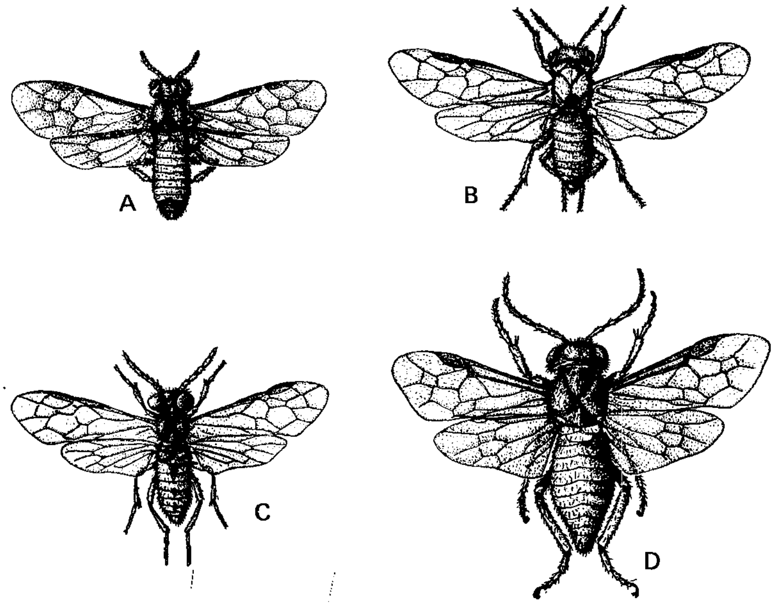

Figure 28–39 Common sawflies (Tenthredinidae). A, the birch leafminer, *Fenusa pusilla* (Lepeletier), male; B, the cherry and hawthorn sawfly, *Profenusa canadensis* (Marlatt), female; C, same, male; D, the raspberry leaf sawfly, *Priophorus morio* (Lepeletier), female. (A, redrawn from Friend and the Bulletin of the Connecticut Agricultural Experiment Station; B and C, redrawn from Parrot and Fulton and the Bulletin of the Geneva, N.Y. Agricultural Experiment Station; D, redrawn from Smith and Kido and Hilgardia.)

body (or the posterior part of it) coiled over the edge of a leaf. There is usually a single generation a year, and the insect overwinters in a pupal cell or cocoon, either in the ground or in a protected situation.

Sawfly larvae feed chiefly on various trees and shrubs, and some are very destructive. The larch sawfly, *Pristiphora erichsonii* (Hartig), is a very destructive pest of larch and, when numerous, can cause extensive defoliation over large areas. The imported currant-worm, *Nematus ribesii* (Scopoli), is a serious pest of currants and gooseberries.

A few species in this group make galls, and a few mine leaves. Species of the genus *Euura* form galls on willow, one of the most common being a small oval gall on the stem. The birch leaf miner (Figure 28–39A), *Fenusa pusilla* (Lepeletier), which makes blotch mines in birch, is a serious pest in the northeastern states. It has two or three generations a year and pupates in the ground. The elm leaf miner, *Fenusa ulmi* Sundevall, mines in elm leaves and frequently does quite a bit of damage.

The family Tenthredinidae is divided into eight subfamilies, separated chiefly on the basis of wing venation. The two sexes are differently colored in many species.

Family **Cephidae—Stem Sawflies:** These are slender, laterally compressed sawflies (Figure 28–40). The larvae bore in the stems of grasses, willows, and berry plants. *Cephus cinctus* Norton bores in the stems of wheat and is often called the "wheat stem sawfly" (Figure 28–40C). The adult is about 9 mm long, shining black, and banded and spotted with yellow. *Cephus cinctus* is an important wheat pest in the western states. A similar species, *C. pygmaeus* (L.), occurs in the east. *Janus integer* (Norton) bores in the stems of currants. The adult is shining black and about 13 mm long. There is a single generation a year, and the insect overwinters in a silken cocoon inside the plant in which the larva feeds. Thirteen species are found in Canada and the United States.

Family **Anaxyelidae—Incense-Cedar Wood Wasps:** This family is represented by only a single living species, *Syntexis libocedrii* Rohwer, which occurs in northern California and Oregon. The adult female is black and 8 mm long. The larva bores in the wood of the incense cedar and Douglas fir, often in trees that have been weakened, for example, by fires.

Family **Siricidae—Horntails:** Horntails are fairly large insects, usually 25 mm or more long, and the larvae are wood-boring. Both sexes have a horny, spearlike plate on the last abdominal segment, and the female has a long ovipositor. Most of the 19 North American species attack conifers, but the most common eastern species, *Tremex columba* (L.), attacks maple, beech, and other hardwoods. *Tremex* is a brown and black insect about 40 mm long (Figure 28–41A). The larvae are seldom sufficiently numerous to do a great deal of damage, and the trees that are attacked are usually old, weakened, or diseased. Pupation occurs in the burrow made by the larva, which ends near the surface of the wood (Figure 28–41B). Species of siricids are sometimes accidentally transported in wood for fuel, construction, or furniture and can occasionally be found well outside their normal geographic range.

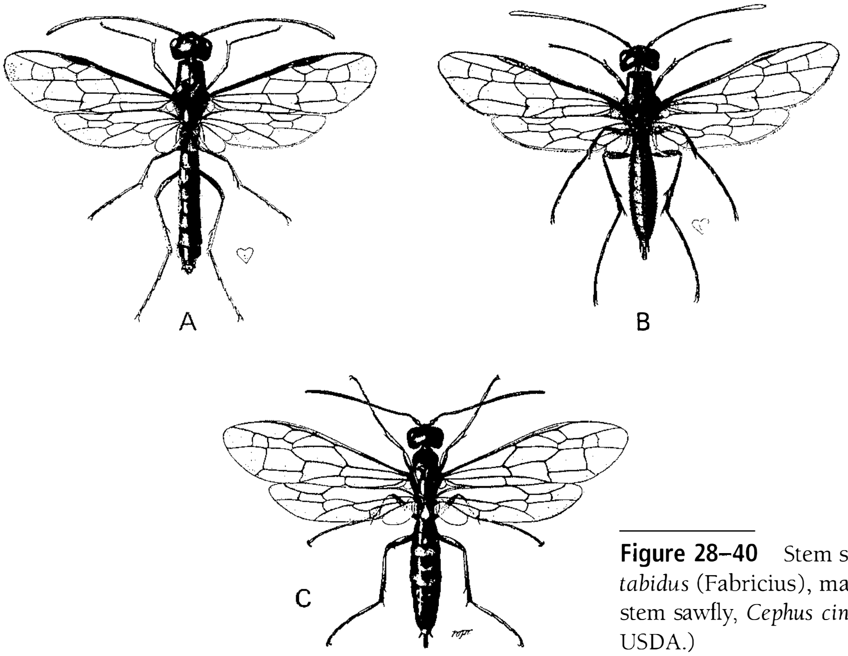

Figure 28–40 Stem sawflies (Cephidae). A, *Trachelus tabidus* (Fabricius), male; B, same, female; C, the wheat stem sawfly, *Cephus cinctus* Norton, female. (Courtesy of USDA.)

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Figure 28–41 A, An adult horntail, *Tremex columba* (L.); B, horntail pupa in the larval gallery.

Family **Xiphydriidae—Wood Wasps**: The wood wasps are small to moderate-sized (5–23 mm long) cylindrical insects somewhat similar to the horntails, but they lack the horny plate at the apex of the abdomen. The larvae bore in small, dead limbs and branches of deciduous trees. There are only 11 North American species, all in the genus *Xiphydria*, and none is very common.

Family **Orussidae—Parasitic Wood Wasps**: This is a small group of rare insects (9 North American species), the adults of which are somewhat similar to horntails but considerably smaller (8–14 mm long). The larvae as far as known are parasites of the larvae of metallic wood-boring beetles (Buprestidae), and possibly other wood-boring Coleoptera and Hymenoptera. These wasps seem to be related to the Apocrita, and some authorities have classified them there or in their own suborder, the Idiogastra. The adults are on the wing from early spring to early summer and can be found searching the trunks of dead and dying trees.

SUBORDER **Apocrita**: The Apocrita differ from the sawflies in having the first abdominal tergum (the propodeum) intimately associated with the thorax and separated by a distinct constriction from the rest of the abdomen. The middle tagma of the body (the mesosoma) is thus four-segmented. In addition, the hind wings have no more than two basal cells, and the fore tibiae have a single apical spur (except the Ceraphronoidea). Apocritan larvae are usually grublike or maggotlike and vary in feeding habits. Most are parasitic or predaceous on other insects, and others are plant feeders. The adults feed chiefly on flowers, sap, other plant materials, and honeydew. Some of the parasitic species occasionally feed on the body fluids of the host (Figure 28–49B).

A great many species in this suborder are parasitic in the larval stage on other insects or other arthropods and, because of their abundance, are very important in keeping the populations of other insects in check. The term *parasitoid* is often used for these insects. Both true parasites and parasitoids live in or on the body of another living animal (the host) during at least part of the life cycle. A parasite usually does not kill its host or consume a large part of the host tissues, but the immature stages of a parasitoid consume all or most of the host's tissues and eventually kill it. In this sense, parasitoids are similar to predators. Most parasitic Apocrita lay their eggs on or in the body of the host, and many have a long ovipositor with which hosts in cocoons, burrows, or other protected situations may be reached. In some cases only a single egg may be laid on the host (solitary parasitism, except in the case of polyembryony, see later); in others several to many eggs may be laid on the same host (gregarious parasitism). Pupation may occur on, in, or near the host, or some distance from it. Some species are thelytokous; that is, females develop from unfertilized eggs, and males are rare or absent altogether. Polyembryony occurs in a few species: A single egg develops into many larvae. Some of the parasitic species are hyperparasites; that is, they attack an insect that is a parasite of another insect.

The superfamilies of Apocrita differ in the form of the pronotum, the character of the ovipositor and antennae, the number of trochanter segments, and the wing venation. Practically all the members of the Stephanidae, Ceraphronoidea, Trigonalyidae, Evanioidea, Ichneumonoidea, Proctotrupoidea, Platygastroidea, Chrysidoidea, Tiphioidea, Scoliidae, and Rhopalosomatidae and most Chalcidoidea and Cynipoidea are parasites of insects or other arthropods. The Apocrita evolved from forms with a piercing ovipositor similar to that of siricoids, but as a rule the females of most parasitic and phytophagous species cannot sting people. In the Chrysidoidea, Apoidea, and Vespoidea, the ovipositor is modified into a sting, whose primary function is to inject venom, either to paralyze its host or prey, or as a defensive mechanism. Females of these groups can often inflict painful wounds. In these species (grouped together as the Aculeata), the egg does not pass through the ovipositor during oviposition, but emerges from its base. The remaining Apocrita are grouped by some authorities in a taxon called either Parasitica or Terebrantes, but this is a heterogeneous paraphyletic grouping.

The Apocrita encompasses by far the majority of species of Hymenoptera, with about 16,000 of the approximately 17,100 North American Hymenoptera species.

***Family* Stephanidae:** The stephanids are a small group (8 North American species) of rare insects that are parasites of the larvae of wood-boring beetles. The adults are 5–19 mm long, slender, and superficially resemble the more common ichneumonids (Figure 28–42A). The head is somewhat spherical, is set out on a neck, and bears a crown of about five teeth around the median ocellus. The hind coxae are long, and the hind femora are swollen and toothed beneath. This group is much more common in the tropics, and most North American species occur in the West. Stephanids have long been classified in the Ichneumonoidea, but they retain many features considered ancestral for the Apocrita as a whole and are now classified in their own superfamily.

***Family* Megaspilidae:** Both this family and the next are unique among the Apocrita in having two fore tibial spurs. Together they form the superfamily Ceraphronoidea. Winged megaspilids can usually be recognized by the large semicircular or ellipsoidal stigma in the fore wing from which arises the curved stigmal vein (Figure 28–19E). A similar venation is found in some dryinids, but megaspilids can be distinguished from them by the triangular shape of the pronotum in lateral view (Figure 28–42B). Some species are wingless or brachypterous; these may be distinguished from ceraphronids by the presence of two middle tibial spurs. There are two subfamilies, the Megaspilinae and the much rarer Lagynodinae. Very little is known of the habits of these wasps; they have been reared from Hemiptera Sternorrhyncha as hyperparasites of other Hymenoptera, from the larvae of Neuroptera and Diptera, and from the puparia of flies. Some *Lagynodes* have been collected in ant nests. One common species, *Dendrocerus carpenteri* (Curtis), is a hyperparasite of the braconid parasites of aphids.

***Family* Ceraphronidae:** Ceraphronids (Figure 28–42C) are distinguished from other Apocrita by the presence of two spurs on the apex of the fore tibia and, usually more easily, by their distinctive wing venation (Figure 28–19G). The veins are highly reduced with a long marginal vein, a linear stigma (separated from the marginal vein by a break), and the curved stigmal vein. Wingless forms are fairly common and can be distinguished from megaspilids

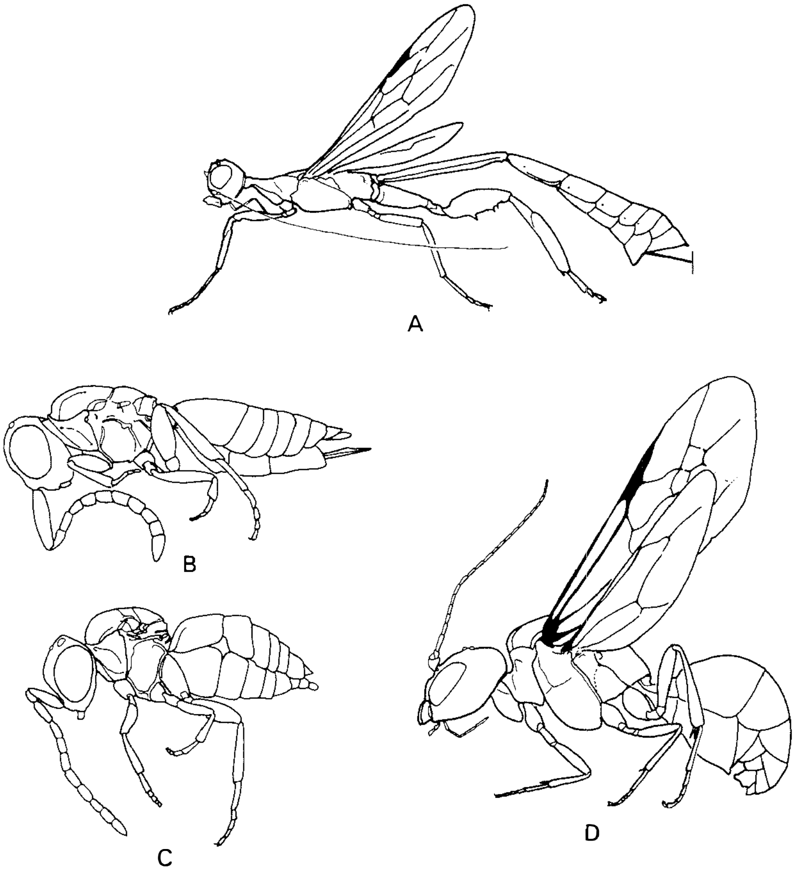

Figure 28–42 A, *Megischus bicolor* (Westwood) (Stephanidae), ovipositor truncated; B, Megaspilidae; C, Ceraphronidae; D, *Taeniogonalos gundlachii* (Cresson) (Trigonalyidae). (A and D redrawn from Townes [1949, 1956].)

by the single spur on the middle tibia. Very little is known of the hosts of ceraphronids, but species have been reared both as primary parasites of Diptera, Neuroptera, and Hemiptera and as hyperparasites of Diptera and Hymenoptera. Some have been collected in ant nests, but their precise hosts are unknown. These creatures are fairly common, but because of their small size they are rarely retained by collectors. Specimens can be easily found by sweeping or by sifting soil and leaf litter.

***Family* Trigonalyidae:** The trigonalyids are a small group (four North American species) of rather rare insects. They are medium-sized, usually brightly colored, and rather stout-bodied. They look much like wasps (Figure 28–42D), but have very long antennae with 16 or more segments.

The trigonalyids are parasites of Vespidae or of the parasites of caterpillars. Some exotic species are primary parasites of sawfly larvae. Females lay large numbers of very minute eggs on foliage. In the case of the species attacking caterpillar parasites, the eggs hatch when eaten by a caterpillar, and the trigonalyid larva attacks the ichneumonid, tachinid, or other parasite larva present inside the caterpillar. In the species that attack vespid larvae, entomologists think the eggs are eaten by a caterpillar, which is in turn eaten by a vespid wasp, which in regurgitating the caterpillar and feeding it to its young, transfers the trigonalyid larvae from the caterpillar to the wasp larvae.

SUPERFAMILY Evanioidea: The members of superfamily Evanioidea have the metasoma attached high above the hind coxae (Figure 28–18D–F), the antennae are filiform, and 13- or 14-segmented, the trochanters are 2-segmented, and the venation is generally fairly complete in the front wings (front wings with a costal cell). Some (Gasteruptiidae and Aulacidae) superficially resemble ichneumonids.

***Family* Evaniidae—Ensign Wasps:** The ensign wasps are black or black and red, somewhat spiderlike insects, 10–25 mm long (Figure 28–43). The metasoma is very small and oval and is attached by a slender petiole to the propodeum considerably above the base of the hind coxae (Figure 28–18F); it is carried almost like a flag (hence the common name for this family). The ensign wasps are parasites of the egg capsules of cockroaches and are likely to be found in buildings or on the forest floor where cockroaches occur.

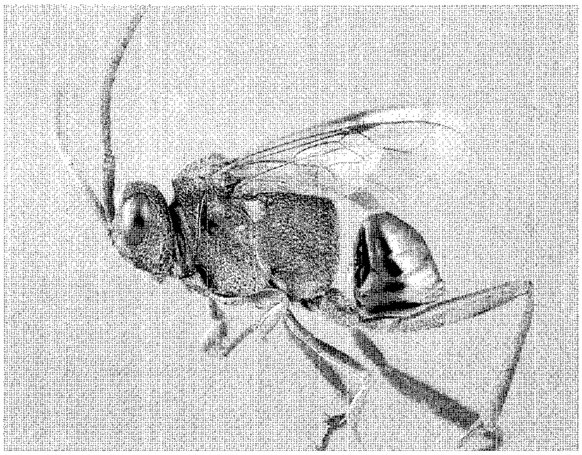

Figure 28–43 An ensign wasp, *Prosevania fuscipes* (Illiger), female.

Family **Gasteruptiidae:** These insects resemble ichneumonids, but they have short antennae and a costal cell in the front wings, and the head is set out on a slender neck. They have one submarginal cell or none and one m-cu crossvein or none (Figure 28–31E). They are generally dark with brown or orange markings. Adults are fairly common and can be found on flowers, particularly wild parsnip, wild carrot, and related species. The larvae are parasites of solitary wasps and bees, and females are often found flying around nesting sites of these hosts, such as dead logs.

Family **Aulacidae:** The aulacids resemble the gasteruptiids, but they are usually black with a reddish metasoma, the antennae are longer, and there are two m-cu crossveins in the front wings (Figure 28–31F). These insects are parasites of the larvae of wood-boring beetles and xiphydriid wood wasps, and adults can be found around logs in which the hosts occur.

SUPERFAMILY Ichneumonoidea: The Ichneumonoidea is a very large and important group, and its members are parasites of other insects or other invertebrate animals. These insects are wasplike in appearance, but (with few exceptions) cannot sting humans. The ichneumonoids are very common insects and may be recognized by the following characters: (1) the antennae are filiform, usually with 16 or more segments; (2) the hind trochanters are 2-segmented; (3) the costal cell is absent; (4) the ovipositor arises anterior to the tip of the metasoma and is permanently exserted (Figure 28–5A; sometimes the ovipositor is very short and does not protrude far beyond the apex of the metasoma); and (5) the pronotum in lateral view is somewhat triangular.

Family **Braconidae:** This is a large (more than 1,900 North American species) and beneficial group of parasitic Hymenoptera. The adults are usually relatively small (Nearctic species are rarely over 15 mm long). They resemble ichneumonids in lacking a costal cell but differ in that they have no more than one m-cu crossvein (Figure 28–31C), and the second and third metasomatic tergites are fused together. Braconid biology is very diverse (Figures 28–44, 28–45). The family contains both ectoparasites and endoparasites, solitary and gregarious species, primary and secondary parasites, and all life stages of host, from egg to adult, may be attacked (in the case of species attacking eggs, the adult wasp emerges from the host larva or prepupa). A small number of tropical species from Central and South America and Australia are phytophagous and form galls. Many species in this family have been of considerable value in controlling insect pests.

The classification of the Braconidae is presently the subject of revision and disagreement. The number of subfamilies recognized in recent works ranges from 29 (Sharkey 1993) to 45 (van Achterberg 1993). Thirty-two subfamilies are found in the Nearctic region (Wharton et al. 1997). The Macrocentrinae, Agathidinae, Cheloninae, Microgastrinae, and most Rogadinae (Rhogadinae), Gnaptodontinae, Dirrhopinae, Miracinae, Acaeliinae, Homolobinae, Sigalphinae, Orgilinae, and Cardiochilinae are parasites of lepidopteran larvae. The gregarious forms of the Macrocentrinae all appear to be polyembryonic. The Cheloninae are egg-larval parasites: The female oviposits into the host egg, and the parasite matures and emerges from the late larva or pupa. Species of *Apanteles* and related genera (Microgastrinae) (Figure 28–45C–E) are very common and often familiar, because the gregarious larvae of some species emerge in large numbers and spin their cocoons in a large mass on the body of the host (Figure 30–78B). The Helconinae, Histeromerinae, Cenocoeliinae, and Doryctinae are parasites of beetle larvae, attacking chiefly wood-boring beetles. The Ichneutinae attack larvae of sawflies and lepidopteran leaf miners; the Alysiinae and Opiinae attack Diptera. Braconinae have been reared from concealed larvae of several orders of Holometabola. The Euphorinae are very diverse biologically: They attack hosts in the orders Lepidoptera, Hemiptera, Hymenoptera, Coleoptera, Neuroptera, and Psocoptera. This subfamily includes species that are parasites of adult insects, as well as hyperparasites. The Aphidiinae is a well-known group that is exclusively endoparasitic in the nymphs and adults of aphids. The Neoneurinae are endoparasites of worker ants. The Blacinae attack primarily the larvae of Coleoptera, but species of one tribe have been reared from boreid larvae (Mecoptera).

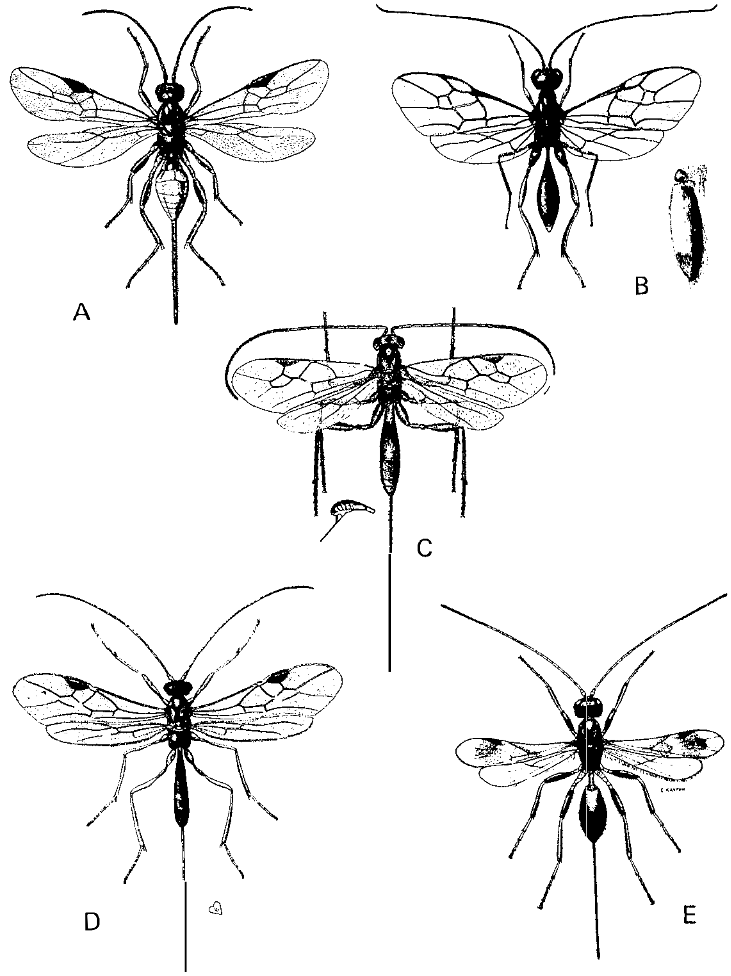

Figure 28–44 Braconidae. A, *Coeliodes dendroctoni* Cushman, female (Braconinae), a parasite of bark beetles (Scolytidae); B, *Meteorus nigricollis* Thomson, male (Euphorinae), a parasite of the European corn borer (insert shows cocoon); C, *Macrocentrus ancylivorus* Rohwer, female (Macrocentrinae) (insert, lateral view of metasoma), a parasite of various tortricid moths; D, *Macrocentrus grandii* Goidanich, female, a parasite of the European corn borer; E, *Spathius canadensis* Ashmead, female, a parasite of bark beetles (Scolytidae). (A, courtesy of DeLeon and the New York Entomological Society; B, courtesy of Parker and the Entomological Society of Washington; C and D, courtesy of USDA; E, courtesy of Kaston and the Connecticut Agricultural Experiment Station.)

***Family* Ichneumonidae—Ichneumonids:** This family is one of the largest in the entire Insecta, with more than 3300 described species in North America, and its members are almost everywhere. The adults vary considerably in size, form, and color, but the majority resemble slender wasps (Figures 28–46, 28–47). They differ from aculeates in that their antennae are longer and have more segments (usually 16 or more antennal segments in ichneumonids and 12 or 13 in most aculeates), and they lack a costal cell in the front wings. In many ichneumonids, the ovipositor is quite long (Figure 28–46A), often longer than the body, and it arises anterior to the tip of the metasoma and is permanently extruded. In the aculeates, the ovipositor issues from the tip of the metasoma and is withdrawn when not in use. In ichneumonids, the 1M and $1R_1$ (first discoidal and first submarginal cells) in the front wing are confluent, owing to the loss of vein Rs+M, and the second submarginal cell (the 1Rs cell), lying opposite the 2m-cu crossvein, is often quite small (Figure 28–31A, are). This small cell (called the *areolet*) is lacking in some ichneumonids (Figure 28–31B). The ichneumonids (with very few exceptions) differ from the braconids in having two m-cu crossveins, the braconids having only one or none (Figures 28–21E, 28–31C). In many species, the two sexes may differ considerably in size, body form, or even the presence of wings.

Most ichneumonids are parasitoids; that is, the larva feeds and develops on a single host that it eventually kills. A few species, however, are better described as mobile predators in that they feed on a number of individual "hosts" before completing development—for example, eggs within a spider egg sac or a line of small carpenter bee larvae within a nest. The hosts of ichneumonids include species in the insect orders Lepi-

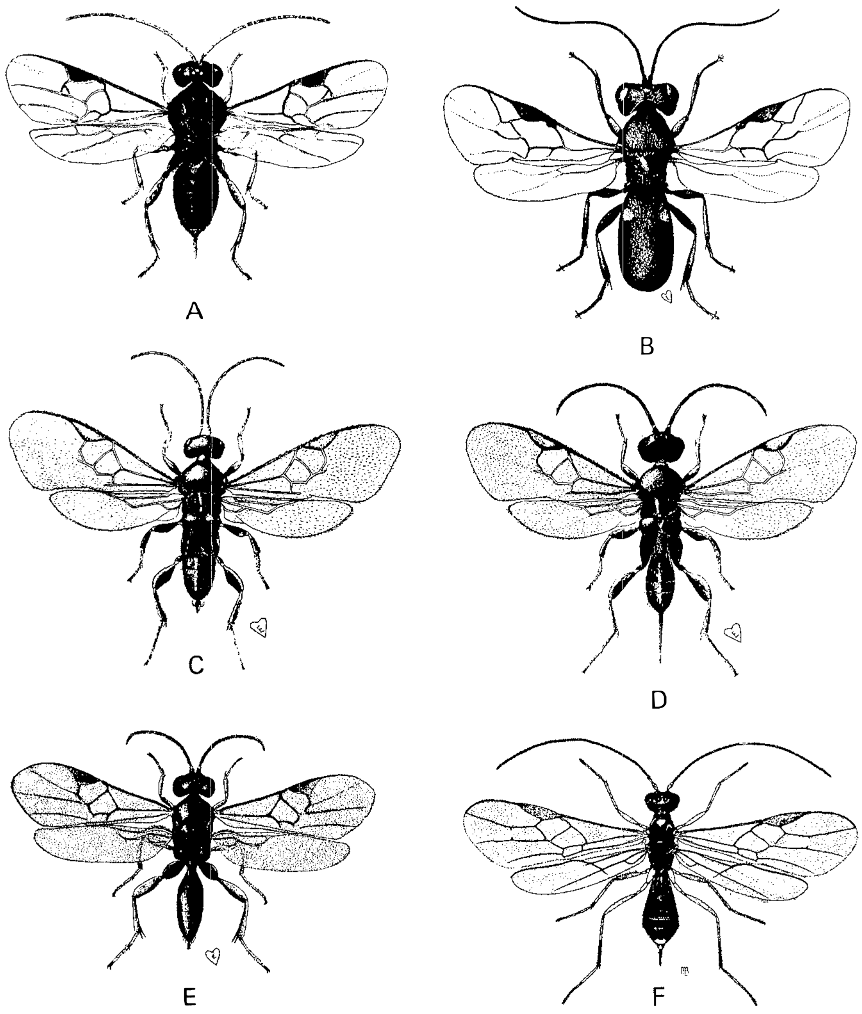

Figure 28–45 Braconidae. A, *Microgaster tibialis* Nees, female (Microgastrinae), a parasite of the European corn borer; B, *Chelonus texanus* Cresson (Cheloninae), a parasite of various noctuid moth larvae; C, *Apanteles diatraeae* Muesebeck, male (Microgastrinae), a parasite of the southwestern corn borer, *Diatraea grandiosella* Dyar; D, same, female; E, *Apanteles thompsoni* Lyle, female, a parasite of the European corn borer; F, *Phanomeris phyllotomae* Muesebeck, female (Rogadinae), a parasite of birch leaf-mining sawflies. (A, courtesy of Vance and the Entomological Society of America; B–F, courtesy of the USDA.)

doptera, Hymenoptera, Diptera, Coleoptera, Neuroptera, and Mecoptera, as well as spiders and spider egg sacs. The host range of individual species is, however, quite variable, some attacking a wide variety and others being highly specialized to one or a few host species. The adult female must locate the host and then may oviposit on, in, or near it (the last in confined situations such as galleries within wood), and the larva may feed on the host from the outside through its cuticle (as an ectoparasite), or it may live within the hemocoel of the host (as an endoparasite). Most ichneumonids are solitary, a single individual developing from a single host, although some are gregarious. Many species are hyperparasitic; that is, they are parasitoids of other parasitoids, usually, ichneumonids, braconids, or tachinids.

The family Ichneumonidae is divided into 24 subfamilies. In the recent past some entomologists disagreed on the nomenclature to be used. In general, the concepts on ichneumonid systematics developed by Townes (1969–1971) are widely followed. We use here the family group names outlined by Fitton and Gauld (1976, 1978).

The largest ichneumonids in the United States and Canada belong to the subfamilies Rhyssinae and Pimplinae. Some may be 40 mm or more in body length, and the ovipositor may be twice as long as the body. These insects attack the larvae of horntails, wood wasps, and wood-boring Coleoptera. The long ovipositor is used in getting the ichneumonid eggs into the host's tunnels, and the ovipositor may sometimes penetrate 13 mm or more of wood. The laborious process of plunging the ovipositor deep within the wood takes several minutes. The egg is greatly deformed as it passes through the valvulae, but regains its shape after emerging from the other end. Retraction of the ovipositor is

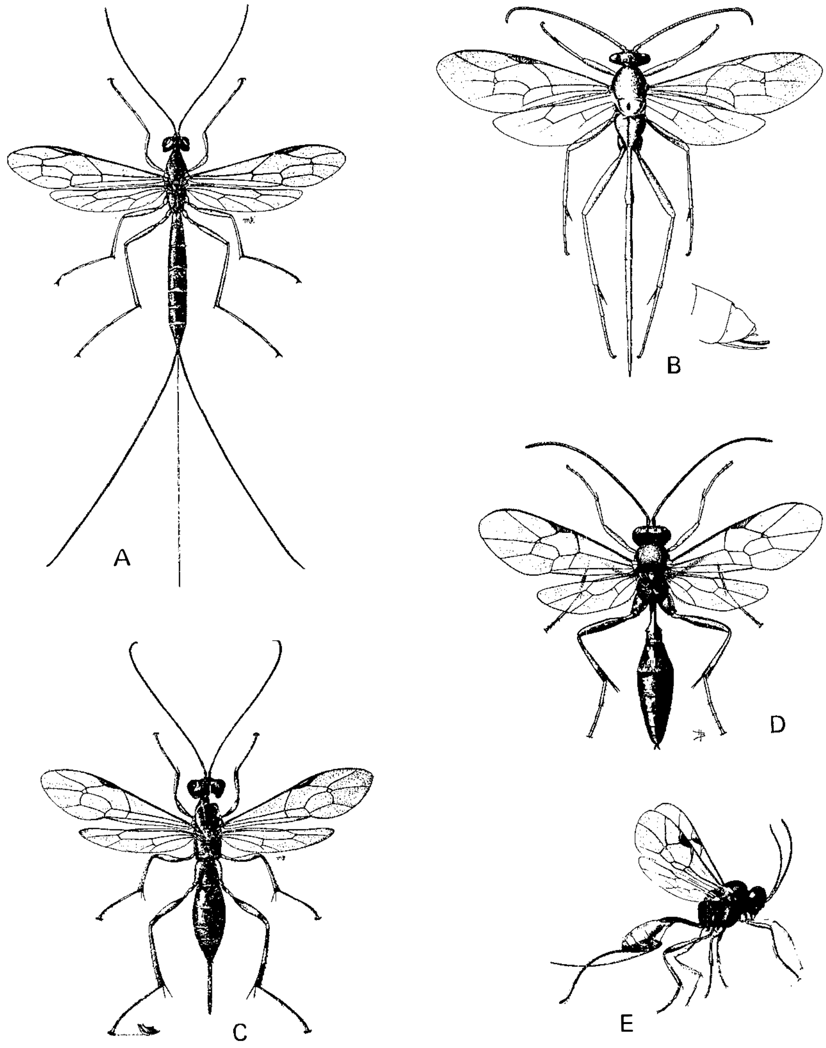

Figure 28–46 Ichneumonidae. A, *Rhysella nitida* (Cresson), female (Rhyssinae); B, *Casinaria ambigua* (Townes), female (Campopleginae) (insert shows tip of metasoma in lateral view); C, *Phytodietus vulgaris* Cresson, female (Tryphoninae); D, *Phobocampe unicincta* (Gravenhorst), female (Campopleginae); E, *Tersilochus conotracheli* (Riley), female (Tersilochinae). (A and C, courtesy of Rohwer; B, courtesy of Walley; D and E, courtesy of the U.S. National Museum.)

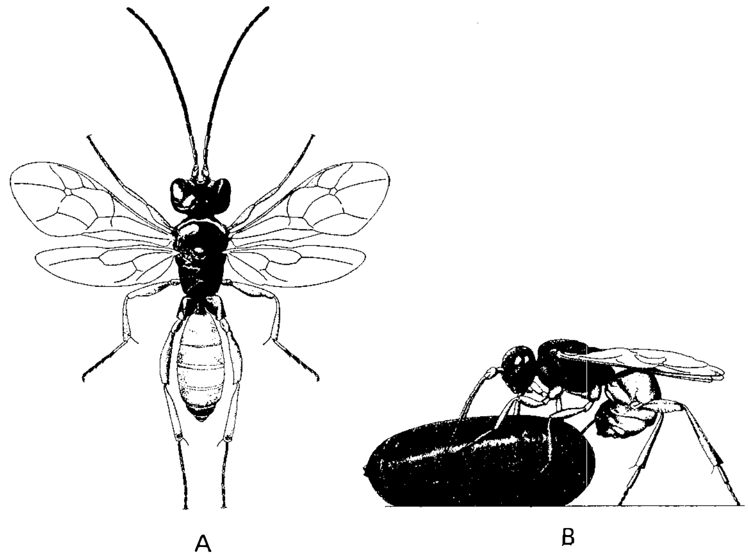

Figure 28–47 A hyperparasitic ichneumonid, *Phygadeuon subfuscus* Cresson (Phygadeuontinae). A, adult male; B, female ovipositing in puparium of the host. The host of this ichneumonid is a tachinid fly, *Aplomyiopsis epilachnae* (Aldrich), which is a parasite of the Mexican bean beetle, *Epilachna varivestis* Mulsant (see Figure 33–72). (Courtesy of USDA.)

also relatively slow. It is not uncommon to find what look like thin, black needles protruding from the wood of a dead tree. These are the ovipositors of females that either were unable to free themselves or were eaten by birds while ovipositing. The genus *Megarhyssa* contains several very large species that attack horntails. *Rhysella nitida* (Cresson) (Figure 28–46A) attacks wood wasps (Xiphydriidae). Some of the other Pimplinae are parasites of lepidopterous larvae, some (especially those in the tribe Polysphinctini) attack spiders, and some attack wood-boring Coleoptera.

Most ichneumonids in the subfamily Tryphoninae are parasites of sawflies. *Phytodietus vulgaris* Cresson (Figure 28–46C) attacks tortricid moths. Some members of this subfamily carry their eggs on the ovipositor, attached by short stalks. When a suitable host is found, the eggs are attached by a stalk to the cuticle of the host, and if no host is found, the eggs may be discarded. The parasite larvae usually complete their development in the host's cocoon.

The members of the subfamily Phygadeuontinae are mostly external parasites of pupae in cocoons. A few attack wood-boring beetle larvae, a few attack dipterous larvae, some attack spider egg sacs, and a few are hyperparasites of braconids or other ichneumonids (Figure 28–47). The members of the subfamily Ichneumoninae are internal parasites of Lepidoptera. They oviposit in either the host larva or the host pupa, but always emerge from the host pupa. In most species in this subfamily, the two sexes appear quite different, and many are bright, colorful mimics of vespids or pompilids. The Banchinae are internal parasites of caterpillars; the Ctenopelmatinae are chiefly parasites of sawflies, ovipositing in the host larva and emerging from its cocoon; the Oxytorinae attack fungus gnats (Mycetophilidae and Sciaridae); and the Diplazontinae attack Syrphidae, laying their eggs in the egg or young larva of the host and emerging from the puparium of the host. The Campopleginae are parasites of lepidopterous larvae. *Casinaria texana* (Ashmead) (Figure 28–46B) is a parasite of the saddleback caterpillar, and *Phobocampe disparis* (Viereck) (Figure 28–46D) is a parasite of the gypsy moth. The Tersilochinae are parasites of beetles. *Tersilochus conotracheli* (Riley) (Figure 28–46E) is a parasite of the plum curculio.

Females of Ophioninae (which are parasites of caterpillars) have a very compressed metasoma and a short, very sharp ovipositor. Most ichneumonids when handled attempt to sting by poking at one's fingers with their ovipositor, but in most cases this can scarcely be felt. The ovipositor of the Ophioninae, in contrast, can actually penetrate the skin, and the effect is much like a sharp pin prick. Most of these ichneumonids are yellowish to brownish and about 25 mm long. They often come to lights at night.

***Family* Mymarommatidae:** This small group of rare species has only recently been discovered in North America. Their hosts are unknown, but specimens have been collected in moist woodlands. They appear similar to the mymarids in having the base of the fore wing constricted and the venation highly reduced (even for a chalcidoid). The hind wing is greatly reduced to a slender strip bearing hamuli on its apex. Recent authors place the mymarommatids outside the Chalcidoidea, in their own superfamily, although recognizing that the two taxa are closely related.

SUPERFAMILY Chalcidoidea: The chalcidoids (superfamily Chalcidoidea) constitute a large and important group of insects, with about 2,200 described North American species. Nearly all are very small, and some are quite minute. Some Mymaridae, for example, are shorter than 0.5 mm. Chalcidoids are to be found almost everywhere, but are so small they are frequently overlooked—or even discarded—by the beginning student. Most are only about 2 or 3 mm long, although a few (for example, some Leucospidae) may reach 10 or 15 mm. The members of this group live in a wide variety of habitats, and a collector can seldom sweep through vegetation without coming up with at least a few of these insects.

The chalcidoids can generally be recognized by the reduced wing venation (Figure 28–19B), the antennae are usually elbowed and never contain more than 13 segments, the pronotum is somewhat quadrate and does not reach the tegulae, and usually a large, exposed prepectus is present in the side of the mesosoma (Figure 28–4A). Most chalcidoids are dark-colored, and many are metallic blue or green. Body shape varies greatly in this group (Figures 28–28, 28–29, 28–48 through 28–53), and some have rather peculiar, even marvelous, shapes. The wings are reduced or lacking in many species.

Most chalcidoids are parasites of other insects, attacking chiefly the egg or larval stage of the host. Most hosts are in the orders Lepidoptera, Diptera, Coleoptera, and sternorrhynchous Hemiptera. because these orders contain most of the crop pests, the chalcidoids are a very beneficial group, helping to keep pest populations in check. Many species have been imported into the United States to control insect pests. A few chalcidoids are phytophagous, their larvae feeding inside seeds, stems, or galls.

This superfamily is divided into a number of families. Some families consist of distinctive-looking insects and are easily recognized, but in some cases separating families is rather difficult. To complicate matters for the student, entomologists differ on the limits of some families.

***Family* Mymaridae—Fairyflies:** Mymarids are all parasites of the eggs of other insects. Their hosts in-

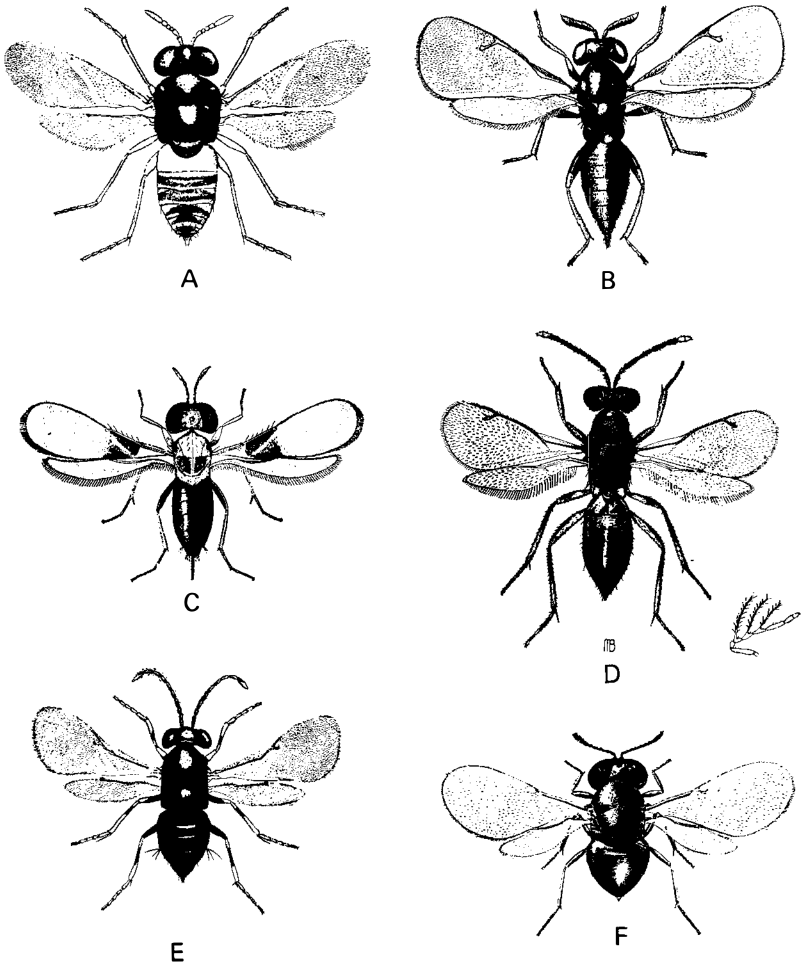

Figure 28–48 Chalcidoidea. A, *Aphelinus jucundus* Gahan, female (Aphelinidae), a parasite of aphids; B, *Baryscapus bruchophagi* (Gahan) (Eulophidae), a parasite of the clover seed chalcid, *Bruchophagus platypterus* (Walker); C, *Centrodora speciosissima* (Girault), female (Aphelinidae), a parasite of cecidomyiids and chalcidoids that attack wheat; D, *Hemiptarsenus fulvicollis* (Westwood), female (Eulophidae), a parasite of leaf-mining sawflies; E, *Zarhopalus inquisitor* (Howard), male (Encyrtidae), a parasite of aphids and mealybugs; F, *Ooencyrtus kuvanae* (Howard), female (Encyrtidae), an imported egg parasite of the gypsy moth. (A and E, courtesy of Griswold and the Entomological Society of America; others, courtesy of USDA.)

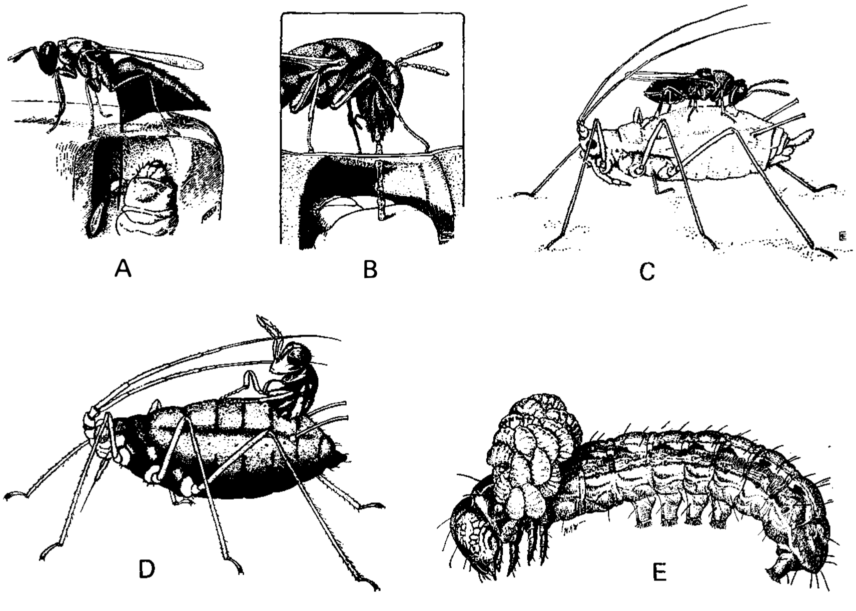

Figure 28–49 Feeding and emerging chalcidoids. A, *Pteromalus* (Pteromalidae) ovipositing; B, *Pteromalus* feeding at the tube made by the ovipositor; C, *Zarhopalus inquisitor* (Howard) (Encyrtidae) feeding at an oviposition puncture made in the abdomen of an aphid; D, adult of *Aphelinus jucundus* Gahan (Aphelinidae) emerging from an aphid; E, a colony of *Euplectrus* larvae (Eulophidae) feeding on a caterpillar. (A and B, courtesy of Fulton and the Entomological Society of America; C and D, courtesy of Griswold and the Entomological Society of America; E, courtesy of USDA.)

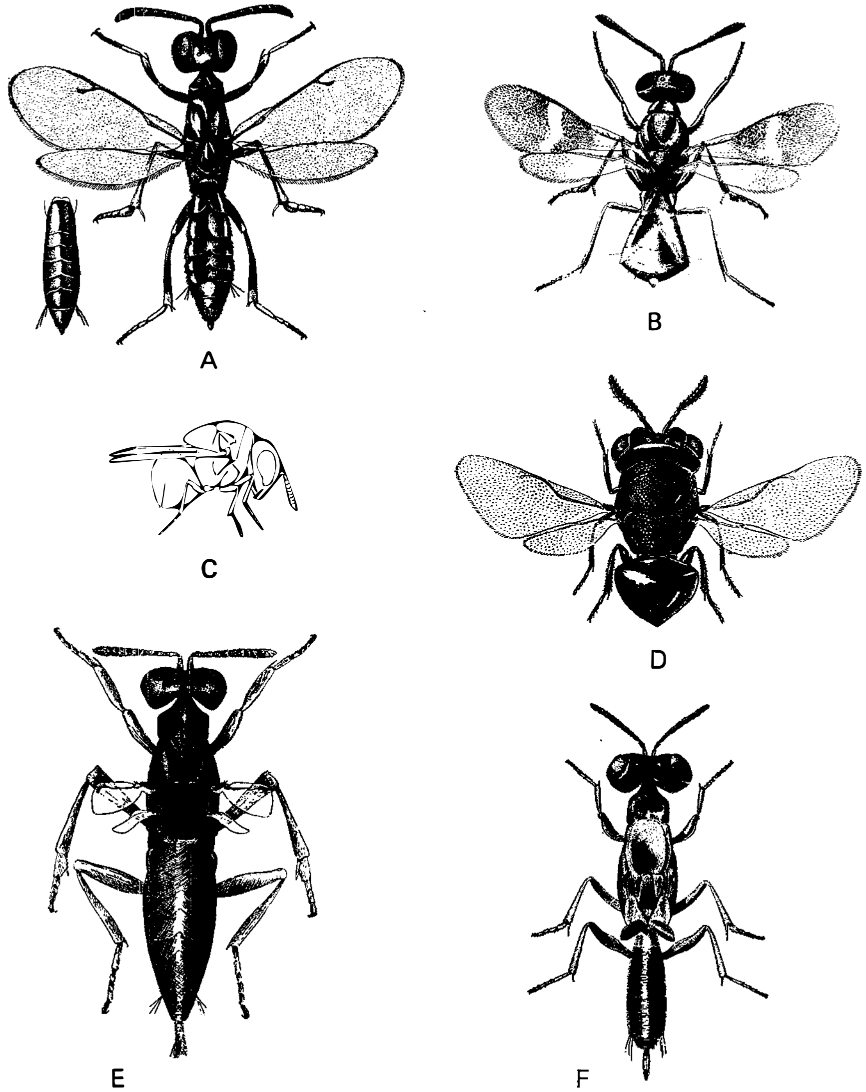

Figure 28–50 Chalcidoidea. A, B, E, F, Eupelmidae; C, D, Perilampidae. A, *Eupelmus allynii* (French), female (insert is the metasoma of male), a parasite of the Hessian fly; B, *Anastatus japonicus* Ashmead, an imported egg parasite of the gypsy moth; C, *Perilampus platygaster* Say, a hyperparasite attacking *Meteorus dimidatus* (Cresson), a braconid parasite of the grape leaffolder, *Desmia funeralis* (Hübner) (Pyralidae), lateral view; D, same, dorsal view; E, *Eupelmus atropurpureus* Dalman, female, a parasite of the Hessian fly; F, *Eupelmus vesicularis* (Retzius), female, which attacks insects in the orders Coleoptera, Lepidoptera, and Hymenoptera. (Courtesy of USDA.)

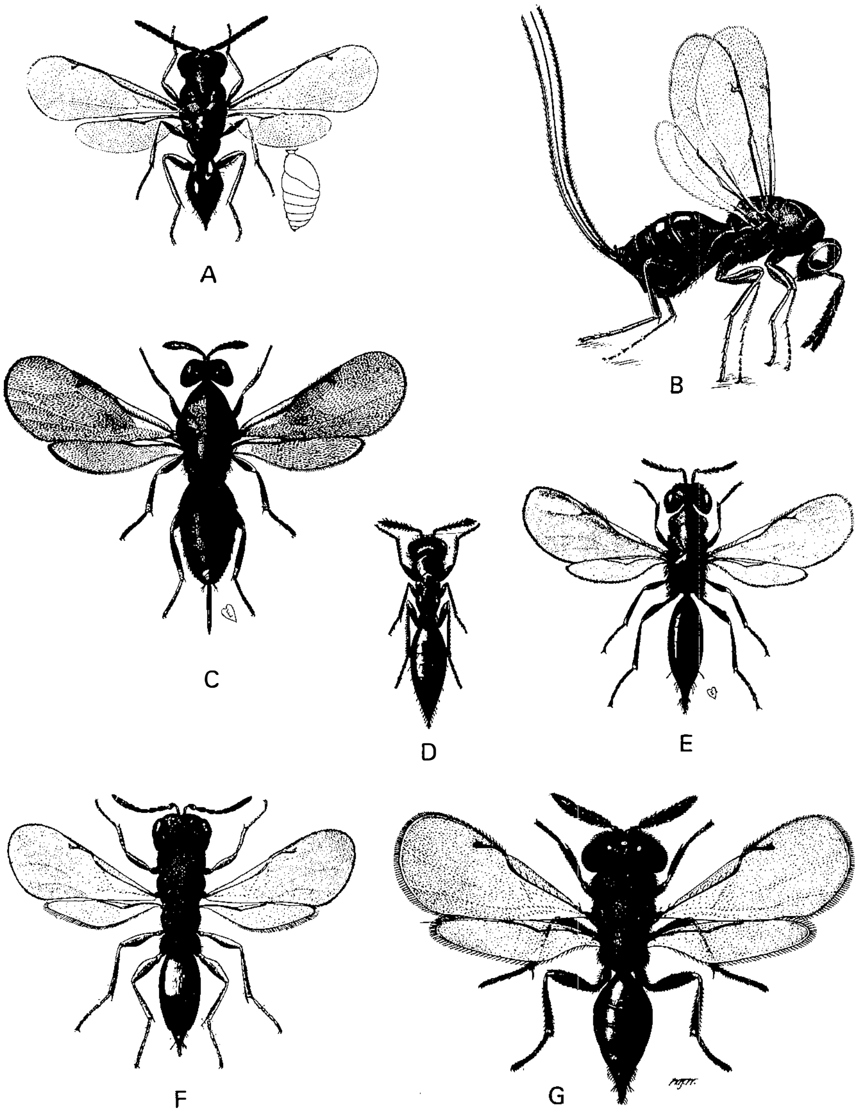

Figure 28–51 Chalcidoidea. A–C, Torymidae; D–G, Eurytomidae. A, *Torymus varians* (Walker), the apple seed chalcid, male (insert is a lateral view of the metasoma); B, same, female; C, *Idiomacromerus perplexus* (Gahan), female, a parasite of the clover seed chalcid (G in this figure); D, *Tetramesa maderae* (Walker), the wheat strawworm, a wingless female; E, *Tetramesa tritici* (Fitch), female, the wheat jointworm; F, *Eurytoma pachyneuron* Girault, female, a parasite of the Hessian fly and the wheat jointworm (E in this figure); G, *Bruchophagus platypterus* (Walker), the clover seed chalcid. (Courtesy of USDA.)

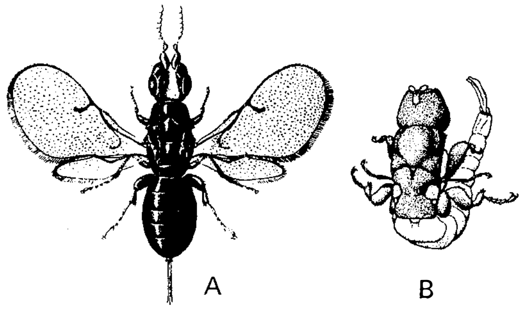

Figure 28–52 The fig wasp *Blastophaga psenes* (L.). A, female; B, male. (Courtesy of Condit and the California Agricultural Experiment Station.)

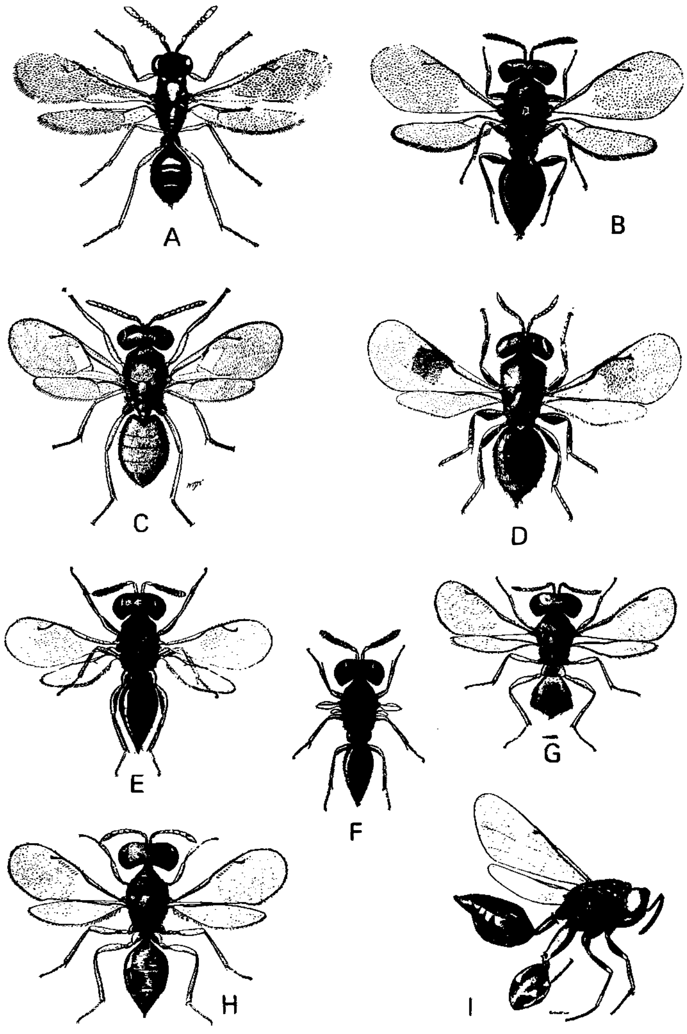

Figure 28–53 Chalcidoidea. A–H, Pteromalidae; I, Chalcididae. A, *Asaphes lucens* (Provancher), male, a parasite of aphids; B, *Thinodytes cephalon* (Walker), female, a parasite of the Hessian fly; C, *Pteromalus eurymi* Gahan, a parasite of the alfalfa caterpillar, *Colias eurytheme* Boisduval; D, *Homoporus nypsius* (Walsh and Riley), female, a parasite of the Hessian fly; E, *Trichomalopsis subaptera* (Riley), female, a parasite of the Hessian fly; F, same, a subapterous female; G, *Callitula bicolor* Spinola, male, a parasite of various flies and platygastrids; H, same, female; I, *Conura side* (Walker) a parasite of various Coleoptera, Lepidoptera, and Hymenoptera. (A, courtesy of Griswold and the Entomological Society of America; B–I, courtesy of USDA.)

clude species in the orders Odonata, Orthoptera, Psocoptera, Thysanoptera, Hemiptera, Coleoptera, Lepidoptera, and Diptera. They are distinguished from all other chalcidoids by a series of unique sulci on the head (Figure 28–24): a set parallel to the inner edges of the compound eyes on the frons and vertex, and a distinctive transverse sulcus running between the eyes above the antennal insertions. In addition, most species are characterized by the stalked, parallel-sided hind wings and the narrow base of the fore wings (Figure 28–19C). These insects are all minute, usually less than 1 mm in size. Consequently, they are poorly known, but they are a common and diverse component of most insect faunas.

***Family* Trichogrammatidae:** The trichogrammatids are also insect egg parasites. They are very small. For example, adults of the genus *Megaphragma*, parasites of the eggs of thrips, are no more than 0.18 mm in total length. Trichogrammatids may be most easily recognized by their three-segmented tarsi. In addition, the metasoma is broadly attached to the mesosoma, and the second phragma projects far within it (visible in specimens in alcohol); the antennae are short, with seven or fewer segments (including ring segments); and the fore wing often has setae arranged in lines (these last three characters also appear in some other chalcidoids). The genus *Trichogramma*, the best known group, has been widely used as a biological control agent. It is, however, not as abundant, either in species or total numbers, as those in the genera *Oligosita*, *Paracentrobia*, and *Aphelinoidea*. As with most other microhymenoptera, even though very common, this family is often overlooked or missed by collectors and is therefore relatively little known.

Family **Eulophidae:** The Eulophidae are a large group (more than 500 described North American species) of rather small insects (1–3 mm long). They are parasites of a wide variety of hosts, including a number of major crop pests (Figures 28–48B,D, 28–49E). Their biology is extremely varied, but most species parasitize either the egg or larva of their host. Eulophids may be recognized by the four-segmented tarsi (Figure 28–23A) and the axillae extending forward beyond the tegulae. Some species of Aphelinidae and Encyrtidae also have four-segmented tarsi. Characters to distinguish these are included in the key and in the discussions of these families. Many eulophids are brilliantly metallic in color, and the males of many species have pectinate antennae. These wasps are, in general, rather weakly sclerotized, and the bodies of specimens often collapse when dried.

Family **Tetracampidae:** This rare family seems to combine features of the larger Eulophidae and Pteromalidae. Some male tetracampids have four-segmented tarsi, but both males and females may be distinguished from other North American eulophids and pteromalids by the dense pilosity on the propodeum. Only two species have been recognized in North America. *Dipriocampe diprioni* (Ferrire), an egg parasite, was introduced into Canada to control the European pine sawfly, *Neodiprion sertifer* (Geoffroy) (Diprionidae). *Epiclerus nearcticus* Yoshimoto occurs in the eastern United States and Canada.

Family **Aphelinidae:** This is a group of very common but small parasites, usually about 1 mm in total length. They have been classified at various times in the Eulophidae and Encyrtidae, but it now seems clear that they should be recognized as an independent family. The number of antennal segments is reduced to eight or fewer (not counting the minute ring segments) as in the Eulophidae, but most species have the tarsi five-segmented, the metasoma appears broadly attached to the propodeum (in many cases the second phragma is visible and extends well into the metasoma), the marginal vein is elongate, and the postmarginal and stigmal veins are reduced. A few encyrtids have four-segmented tarsi and reduced antennal segmentation; aphelinids can be distinguished from these by their elongate marginal vein. Those species of aphelinids with five-segmented tarsi (the majority) can be distinguished from encyrtids by the reduced number of antennal segments, their small size, reduced stigmal and postmarginal veins, and the presence of a groove on the mesopleuron for receiving the middle femur.

Aphelinids attack a broad range of hosts, which all seem to be sessile. The best known species are those that attack scale insects (Hemiptera). A number of species have been very important as agents of biological control of these scale hosts. Other species have been reared from aphids; whiteflies; eggs of Hemiptera, Orthoptera, and Lepidoptera; cecidomyiid pupae; and as hyperparasites of other Hymenoptera attacking Hemiptera. The curious phenomenon of adelphoparasitism is found in some groups: The females develop as parasites of scale insects, whereas the males develop as hyperparasites attacking parasites of scale insects, often females of their own species! This fairly common group of parasites is generally not represented in collections because they are so small and because the bodies usually collapse when dried.

Family **Signiphoridae:** The signiphorids are small, stout-bodied chalcidoids that attack scale insects, whiteflies, and other sternorrhynchous Hemiptera or are hyperparasites of the chalcidoids attacking these Hemiptera. They are rather uncommon but very distinct creatures because of the broad attachment of the metasoma, the elongate, unsegmented antennal club, the lateral spurs on the middle tibia, and the triangular area on the propodeum.

Family **Encyrtidae:** The Encyrtidae are a large and widespread group, with some 345 described North American species. They are usually 1–2 mm long and can be distinguished from most other chalcidoids by the broad, convex mesopleura (Figure 28–27A). In most chalcidoids, the mesopleura have a groove for the femora, but encyrtids lack this groove (as do the signiphorids, tanaostigmatids, some aphelinids, and some eupelmids). The encyrtids differ from the eupelmids in having the fore and middle coxae closely approximated, the mesonotum is convex, and in lacking notauli or having them incomplete. Most encyrtids are parasites of sternorrhynchous Hemiptera—aphids (Figure 28–49C), scale insects, mealybugs, and whiteflies—and they are very important as biological control agents of these insects. The group also contains species attacking insects in the orders Neuroptera, Diptera, Lepidoptera, Coleoptera, and Hymenoptera. All life stages, including eggs, larvae, nymphs, and adults are hosts of various species. Two genera in particular, *Hunterellus* and *Ixodiphagus*, are remarkable because they parasitize the nymphal stage of ticks. The genus *Ooencyrtus* is common; its species are parasites of the eggs of some Hemiptera, Neuroptera, and Lepidoptera. *Ooencyrtus kuvanae* (Howard) (Figure 28–48F; also known in the literature as *O. kuwanai*), for example, has been introduced as a parasite of the eggs of the gypsy moth. A few encyrtids are hyperparasites. Polyembryony occurs in a number of species, with from 10 to more than 1,000 young developing from a single egg.

Family **Tanaostigmatidae:** Four species in this rare group have been recorded from Florida, Arizona, and California. The larvae appear to be gall makers.

Family **Eupelmidae:** The Eupelmidae are a large group (88 North American species), and some species are fairly common. They are similar to the encyrtids, but they have a flatter mesonotum and have notauli (Figure 28–50A,B,E,F). Some are wingless or have very short wings (Figure 28–50E,F). Males of many species are very similar to, if not indistinguishable from, male pteromalids.

Many eupelmids are good jumpers and often tumble around after jumping, before gaining a foothold. Their jumping is accomplished by greatly enlarged leg muscles that insert on the mesopleuron. The enlargement of the area of attachment of these muscles accounts for the characteristic convex mesopleuron of both encyrtids and eupelmids. When eupelmids jump, the middle legs are literally thrown out of their sockets and the mesonotum is contorted so strongly that the head and tip of the metasoma may actually touch over the back of the animal. Many specimens retain this position when killed, with the body in a U shape and the middle legs thrown forward in front of the head. The species of this group attack a wide variety of hosts, and a number attack hosts in several different orders. Species of the most common subfamily, the Eupelminae, can be collected in a wide variety of habitats. The less common subfamilies are often seen on dead wood, presumably searching for wood-boring Coleoptera as hosts.

***Family* Torymidae:** The torymids are somewhat elongate insects, 2–4 mm long, generally with a long ovipositor. The hind coxae are usually very large, and there are distinct notauli on the mesoscutum (Figure 28–51A–C). This group includes both parasitic and phytophagous species: The Toryminae, Erimerinae, and Monodontomerinae attack gall insects and caterpillars, the Podagrioninae attack mantid eggs, and the Idarninae and Megastigminae attack seeds.

***Family* Agaonidae—Fig Wasps:** This group is represented in the United States by two species, *Blastophaga psenes* (L.) and *Secundeisenia mexicana* (Ashmead). The former occurs in California and Arizona, and the latter in Florida. *Blastophaga psenes* (Figure 28–52) was introduced into the United States to make possible the production of certain varieties of figs. The Smyrna fig, which is grown extensively in California, produces fruits only when pollinated with pollen from the wild fig, or caprifig, and the pollination is done entirely by fig wasps. The fig wasp develops in a gall in the enclosed flowers of the caprifig. The blind and flightless males (Figure 28–52B) emerge first and may mate with females still in their galls. The female, on emerging from the gall, collects pollen from male flowers of the caprifig and stores it in special baskets (corbiculae). The female pollinates figs of both types (Smyrna fig and caprifig), but oviposits successfully only in the shorter flowers of the caprifig. Fig growers usually aid Smyrna fig pollination by placing branches of the wild fig in their cultivated fig trees. When the fig wasps emerge from the wild fig, they are almost certain to visit flowers of the Smyrna fig and thus pollinate them.

***Family* Ormyridae:** The Ormyridae are similar to the Torymidae, but have the notauli indistinct or lacking and have a very short ovipositor. Most species are metallic blue or green and have distinctive large pits on the metasomatic segments. They are parasites of gall insects.

***Family* Pteromalidae:** The Pteromalidae is a huge group of parasitic wasps (about 340 described North American species). The bulk of the species are placed in two large and poorly defined subfamilies, the Miscogastrinae and Pteromalinae. In addition, a large number of small but distinctive groups are usually given subfamily status (for example, the Spalangiinae, common parasites of the puparia of flies associated with dung). Other groups, such as the Perilampidae and Eucharitidae, are commonly accorded familial status, but entomologists recognize these as being closely related to subgroups within pteromalids. The classification of these wasps is in a very immature stage, and a fair amount of shuffling of taxa should be expected as the species and their relationships become better known.

The pteromalids are both morphologically and biologically diverse. It is probably easier to identify them by eliminating the other possibilities than to try to characterize the family. In general, the tarsi have five segments, the antennal funicle has five or more segments, and the pronotum, seen in dorsal view, is constricted anteriorly (giving it the shape of a bell, often referred to as *campanulate*). Although females of some families such as Eupelmidae and Torymidae are often quite distinctive, it may sometimes be difficult, if not impossible, to distinguish the males from "typical" pteromalids. The best strategy for identification is to first run specimens through the key and then check the descriptions and key characters of the other chalcidoid taxa. The others with five-segmented tarsi are the Perilampidae, Eupelmidae, Encyrtidae, Tanaostigmatidae, Chalcididae, Leucospidae, Eurytomidae, Eucharitidae, Agaonidae, Torymidae, Ormyridae, and Aphelinidae.

Most of these insects are parasitic and attack a wide variety of hosts. Many are very valuable in the control of crop pests. Some species attack eggs, larvae, nymphs, and pupae. Both solitary and gregarious parasites are found, and some species are hyperparasitic. Hosts include species in the orders Lepidoptera, Hymenoptera, Hemiptera, Diptera, and Coleoptera, and spiders and their egg sacs. A few species form galls.

The adults of some species of pteromalids (and some other chalcidoids, such as some eulophids) feed on the body fluids of the host, which exude from the puncture made by the parasite's ovipositor (as in Figure 28–49C). In the case of *Pteromalus cerealellae*

(Ashmead), which attacks larvae of the Angoumois grain moth and in which the larvae are out of reach of the adult pteromalid (in the seed), a viscous fluid is secreted from the ovipositor and is formed into a tube extending down to the host larva. Through this tube the adult sucks up the body fluids of the host (Figure 28–49A,B).

Family **Eucharitidae:** The Eucharitidae are rather distinctive-looking insects with very interesting habits. They are fair-sized (at least for a chalcidoid), usually black or metallic blue or green, with the metasoma petiolate and the scutellum often spined. The mesosoma often appears somewhat humpbacked (Figure 28–28D). These chalcidoids are parasitoids of ant pupae. The eggs are laid, usually in large numbers, on leaves or buds, and hatch into tiny, flattened larvae called *planidia*. These planidia simply lie in wait on the vegetation or on the ground and attach to passing ants, which carry them to the ant nest. Once in the ant nest, the planidia leave the worker ant that brought them there and attach to ant larvae. They do little or no feeding on the larvae of the ant, but feed after the larva has pupated. This family is especially diverse in species and in elaborate structure in the tropics where ants are most diverse.

Family **Perilampidae:** The Perilampidae are stout-bodied chalcidoids with the mesosoma large and coarsely punctate and the metasoma small, shining, and triangular (Figures 28–29B, 28–50C,D). Some species, including the common *Perilampus hyalinus* Say, are brilliantly metallic in color and superficially resemble cuckoo wasps (Chrysididae); most others are black. Perilampids are frequently found on flowers. Some species are hyperparasites, attacking the Diptera and Hymenoptera that are parasites of caterpillars and grasshoppers. Others attack free-living insects in the orders Neuroptera, Coleoptera, and Hymenoptera (sawflies). The perilampids, like the eucharitids, lay their eggs on foliage, and the eggs hatch into planidial larvae (small, flattened, able to go without feeding for a considerable time). These planidia remain on the foliage, attach to a passing host (usually a caterpillar), and penetrate into its body cavity. If a hyperparasite enters a caterpillar that is not parasitized, it usually does not develop. If the caterpillar is parasitized, then the perilampid larva usually remains inactive in the caterpillar until the caterpillar parasite has pupated, and then attacks the parasite.

Family **Eurytomidae—Seed Chalcidoids:** The eurytomids are similar to the perilampids in having the pronotum and mesoscutum coarsely punctate, but differ in having the metasoma rounded or oval and more or less compressed (Figures 28–29C, 28–51D–G). The metasoma of males is often strongly petiolate. They can be distinguished from pteromalids by the quadrate shape of the pronotum in dorsal view and by the coarsely punctate mesosoma. They are usually black, but may be yellow or even metallic in color. They are generally more slender in build than the perilampids. Eurytomids vary in habits. Many are parasitic, but some are phytophagous. The larvae of species in the genus *Tetramesa* (Figure 28–51D,E) feed in the stems of grasses, sometimes producing galls on the stems. Some are often serious pests of wheat. The clover seed chalcid, *Bruchophagus platypterus* (Walker) (Figure 28–51G), infests the seeds of clover and other legumes. A few species are hyperparasitic.

Family **Chalcididae:** The Chalcididae are fair-sized chalcidoids (2–7 mm long) with greatly swollen and toothed hind femora (Figures 28–23E, 28–29A, 28–53I). They differ from the leucospids in having the ovipositor short and the wings not folded longitudinally when at rest. Pteromalids in the subfamily Chalcedectinae also have enlarged hind femora, but these species are metallic in color. Chalcidids are usually black or yellow with various markings, but never metallic. Similarly, Podagrioninae (Torymidae) have enlarged hind femora, but like most other chalcidoids, these have a large and exposed prepectus. The prepectus of chalcidids is quite small and mostly hidden internally.

The chalcidids are parasites of Lepidoptera, Diptera, and Coleoptera. Some are hyperparasitic, attacking tachinids or ichneumonids.

Family **Leucospidae:** The Leucospidae are usually black- or brown-and-yellow insects, and they are parasites of bees and wasps. They are rather uncommon but may occasionally be found on flowers. They are stout-bodied; many have the wings folded longitudinally at rest; and they look a little like a small vespid. The ovipositor in most species is long and curves upward and forward over the metasoma, ending over the posterior part of the mesosoma. Like the chalcidids, the leucospids have the hind femora greatly swollen and toothed on the ventral side.

SUPERFAMILY **Cynipoidea:** The members of the superfamily Cynipoidea are mostly small or minute insects with distinctively reduced wing venation (Figure 28–19A). Most species are black, and the metasoma is usually somewhat laterally compressed. The antennae are filiform, the pronotum extends back to the tegulae, and the ovipositor issues from the anterior to the apex of the metasoma. In the fore wing, the marginal cell (cell R_1) is usually well developed. Of the more than 800 species in this group in the United States, some 640 (all in the subfamily Cynipinae) are gall makers or gall inquilines. The others, as far as is known, are parasites.

Family **Ibaliidae:** The ibaliids are relatively large (7–16 mm long) yellow and black insects. They have a somewhat elongate metasoma, and the marginal cell in the fore wing is distinctively elongate. They are parasites of horntails (Siricidae) and can most easily be found on or about logs containing these hosts.

***Family* Liopteridae:** These insects have the metasoma petiolate and attached far above the bases of the hind coxae. Three rare species occur in Texas and California. Their immature stages are unknown.

***Family* Figitidae:** This is a diverse group, and its species are parasites of a variety of groups. Five subfamilies are represented in the North American area. The Anacharitinae, which have the metasoma distinctly petiolate and the second tergum longer than the third (Figure 28–20E), attack the cocoons of lacewings (Chrysopidae). The Aspiceratinae, in which the second metasomatic tergum is narrow and much shorter than the third (Figure 28–20C), attack the pupae of syrphid flies. The Charipinae are parasites of psyllids (Hemiptera) and hyperparasites of aphids, attacking Braconidae and Aphelinidae (Hymenoptera). The Figitinae, in which the second tergum is only slightly shorter than the third (Figure 28–20F), attack the pupae of Diptera. The subfamily Eucoilinae can be recognized by the rounded, cuplike elevation on the scutellum (Figure 28–20D). This structure is at times quite elaborate, and the scutellum may also be developed in a posterior spine. Eucoilines are parasites of the pupae of flies.

***Family* Cynipidae—Gall Wasps:** The gall wasps (Figure 28–54) are a large group, and many species are quite common. Within the subfamily are species that are either gall makers or gall inquilines (in rare cases, possibly either). Most species of gall makers attack oaks (*Quercus*) or members of the rose family (Rosaceae) (Figure 28–55). The female wasp oviposits into meristematic tissue that is or will be actively growing the next spring—for example, buds of twigs, flowers, or leaves. The feeding of the wasp larva somehow causes a growth reaction in the host plant that forms a gall. The wasp larva feeds on the elaborated gall tissue, pupates within this enclosure, and chews an exit hole to emerge. The galls themselves come in a wide variety of forms, the shape being determined by the species of gall wasp feeding within. Many galls are quite large and apparent, as in the various types of oak leaf galls, but some are formed within stems or twigs or even underground on the roots (some wasp species burrow down more than 1 meter to oviposit on oak roots), and so these are not apparent to a casual observer. Many galls are dehiscent; that is, they fall off the host plant to the ground with the gall maker still within. Some galls even continue to grow after falling!

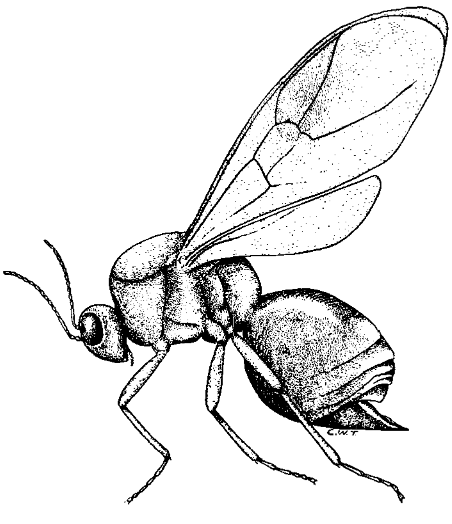

Figure 28–54 A gall wasp, *Diplolepis rosae* (L.). This species develops in the mossy rose gall (Figure 28–55D).

The life cycles of many gall makers are very complex. Some species are very similar to other Hymenoptera: They are bisexual, males and females emerge from their galls and mate, mated females then seek out hosts in which to oviposit; fertilized eggs develop into females, unfertilized eggs into males (arrhenotokous parthenogenesis). Cynipids with this type of life cycle are typically univoltine and attack a wide variety of plants other than oaks and roses. Some species with this general type of life cycle have abandoned the production of males and reproduce by means of thelytokous parthenogenesis. In these the eggs fail to complete meiosis and develop into diploid females; males are rare or entirely absent.

From this point, yet further complications are found. Some species alternate sexual and asexual generations. The sexual generation consists of males and females. These emerge and mate, and the females search out a host in which to oviposit. However, all her progeny develop into females (the so-called agamic generation). After the agamic generation completes its larval development, the adult wasps emerge, find a host, and oviposit. Some unfertilized eggs develop into males of the sexual generation, some into females. In some species, the offspring of a given agamic female are all males, and another's all develop into females. The genetic mechanisms by which the sex of the larvae of the sexual generation is determined are very poorly understood. The adult wasps of the sexual and agamic generations are usually very different in morphology and produce different types of galls on different parts of the host plant. In some cases the two generations must reproduce on different species of hosts. As a result, the sexual and agamic generations have typically been described as separate species of gall wasps, sometimes even in different genera.

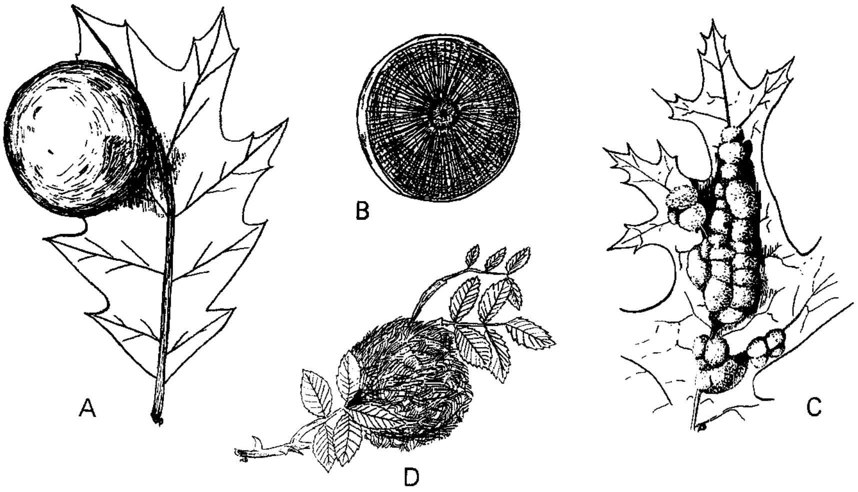

Figure 28–55 Galls of Cynipidae. A, an oak-apple gall, caused by *Amphibolips* sp.; B, another oak-apple gall, cut open to show the interior and the central capsule in which the gall wasp larva develops; C, the woolly oak gall, caused by *Callirhytis lanata* (Gillette); D, the mossy rose gall, caused by *Diplolepis rosae* (L.). (Redrawn from Felt [1940].)

The inquiline species have somehow lost the ability to induce the host plant to produce galls. These wasps oviposit into galls produced by other species, and their larvae feed on the elaborated gall tissue. The inquiline larvae do not normally seem to feed directly on the original gall-making larva, but the latter often does not survive to emerge.

SUPERFAMILY **Proctotrupoidea:** All the members of this superfamily are parasites, attacking the immature stages of other insects. Most are small or minute, and black, and they may be confused with cynipoids, chalcidoids, or some of the aculeates. The smaller members of this group have a much reduced wing venation, but they may be distinguished from chalcidoids by the structure of the mesosoma and ovipositor. The pronotum in the proctotrupoids appears triangular in lateral view and extends to the tegulae, and the ovipositor issues from the tip of the metasoma rather than from anterior to the tip.

Family **Pelecinidae:** The only North American species in this group is *Pelecinus polyturator* (Drury), a large and striking insect. The female is 50 mm or more long and shining black, with a very long and slender metasoma (Figure 28–56). The male, which is extremely rare, is about 25 mm long and has a swollen posterior part of the metasoma. Males in the southern part of the distribution of this species, from Mexico to Argentina, are quite common. When captured, the female swivels her metasomatic segments and thrusts with the ovipositor, but they rarely penetrate the skin. This insect is a parasite of the larvae of june beetles (Scarabaeidae), and the adults emerge in middle to late summer.

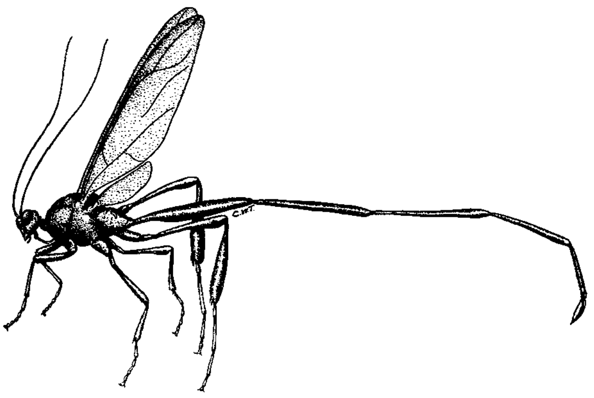

Figure 28–56 A pelecinid, *Pelecinus polyturator* (Drury), female, 1½×.

Family **Vanhorniidae:** This family is closely related to the Proctotrupidae and contains only one species in North America, in the east. *Vanhornia eucnemidarum* Crawford is a parasite of the larvae of eucnemid beetles. *Vanhornia* is characterized by its exodont mandibles—that is, the apical teeth point laterally rather than mesally (Figure 28–22D)—and by a long ovipositor that is curved forward beneath the body of the female.

Family **Roproniidae:** This family contains three rare North American species of *Ropronia*. The adults are 8–10 mm long and have a laterally flattened, somewhat triangular and petiolate metasoma and a fairly complete venation in the front wing (Figures 28–21F, 28–57). The immature stages are parasites of sawflies.

Family **Heloridae:** This family contains two species in North America, *Helorus anomalipes* Panzer and *H. ruficornis* Foerster. These black insects are about 4 mm long, with a fairly complete venation in the front wings (Figures 28–21H, 28–58). Both are parasites of the larvae of lacewings (Chrysopidae), and the adult helorid emerges from the host cocoon.

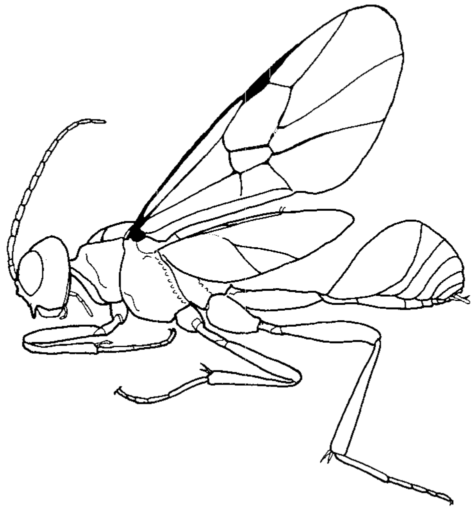

Figure 28–57 *Ropronia garmani* Ashmead. (Redrawn from Townes [1948].)

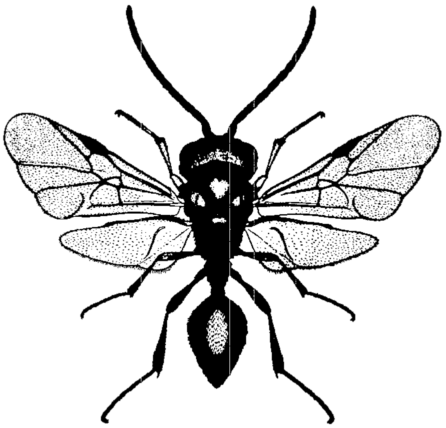

Figure 28–58 *Helorus anomalipes* Panzer female (Heloridae). (Courtesy of Clancy and the University of California.)

Family **Proctotrupidae:** Most Proctotrupidae are 3 to 6 mm long (some are larger). The Nearctic species can be recognized by the large stigma in the front wing, beyond which is a very narrow marginal cell (Figure 28–21D). As far as is known, they are solitary and gregarious parasites of the larvae of Coleoptera and Diptera. The wasp larvae consume their host and then pupate with the end of the metasoma still inside the remains of the host (this also occurs in Pelecinidae).

Family **Diapriidae:** The diapriids are small to minute insects, most of which are parasites of immature Diptera. They can usually be recognized by the shelflike protuberance, in about the middle of the face, from which the antennae arise (Figure 28–59). The family contains four subfamilies. The Ambositrinae are most diverse in the southern continents of Australia (and New Zealand), South America, and southern Africa (and Madagascar). Only a single species extends its range into the Nearctic: *Propsilloma columbianum* (Ashmead) is found as far north as southern Canada. The Ismarinae are recognized by the absence of the typical diapriid frontal shelf; 11 species occur in the United States and Canada and, as far as is now known, these are hyperparasites of dryinids. Most of the approximately 300 North American species in the family belong to just two subfamilies, the Diapriinae and the Belytinae. The Diapriinae are small to minute and have very reduced wing venation, with no closed cells in the hind wings (Figure 28–19D). Most are parasites of Diptera, but some are associated with ants (in a few cases, parasitic on the ants; in many cases entomologists do not know whether the Diapriinae parasitize the ants or other ant associates). The Belytinae are usually larger and have a closed cell in the hind wings (Figure 28–31G). Diapriids are easily collected by sweeping. The Belytinae are very common in moist, wooded areas, because they attack fungus gnats (Mycetophilidae) and other flies breeding in fungi.

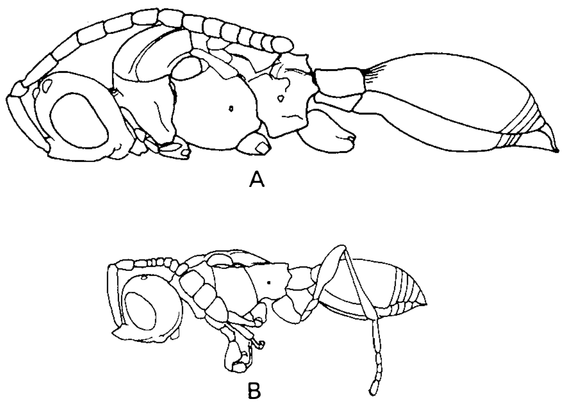

Figure 28–59 Diapriidae. A, Belytinae; B, Diapriinae.

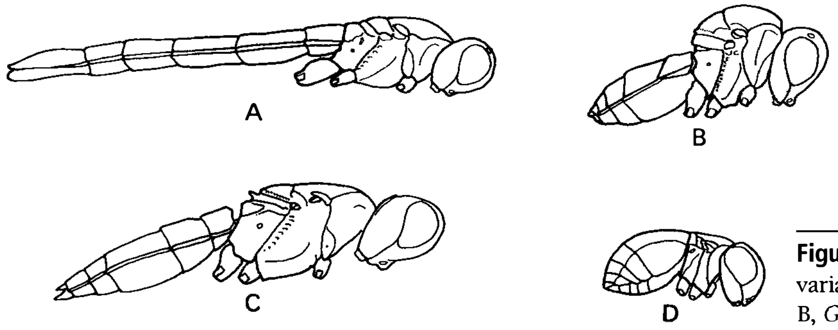

Figure 28–60 Scelionidae, illustrating variation in body form. A, *Macroteleia*; B, *Gryon*; C, *Baryconus*; D, *Baeus*.

SUPERFAMILY **Platygastroidea:** Only two families make up this group, the Scelionidae and Platygastridae. They were previously classified in the Proctotrupoidea, but recently have been separated from those families. The ovipositor of the female is extruded by hydrostatic pressure in the metasoma, sometimes assisted by muscles inserting on the base of the ovipositor.

***Family* Scelionidae:** The Scelionidae are small insects that are parasites of the eggs of spiders and insects in the orders Orthoptera, Mantodea (in the Old World and Australia), Hemiptera, Embiidina, Coleoptera, Diptera, Lepidoptera, and Neuroptera. Some have been successfully used in controlling crop pests.

The eggs of the hosts of scelionids vary in shapes and sizes, and the wasps themselves are quite diverse in body form (Figure 28–60). For example, the genus *Macroteleia* parasitizes the eggs of Tettigoniidae (Orthoptera), and the wasps are relatively large and elongate. *Baeus*, in contrast, attacks the spherical eggs of spiders, and the wingless females are almost spherical themselves. Most scelionids have the metasomatic segments divided into a large median sclerite and narrow laterotergites or laterosternites. These latter structures interlock to form a sharply angled margin on the metasoma. However, several genera of scelionines and the entire subfamily Telenominae have reduced or absent laterosternites and greatly enlarged laterotergites. As a consequence, the metasoma of these species is rounded laterally. In most species the antennae are 12-segmented in both sexes, but varying degrees of reduction in the number of segments are common. Telenomine females have either 11- or 10-segmented antennae. As an extreme, the females of *Idris, Baeus,* and related genera have 7-segmented antennae with a large, unsegmented clava. In the females of a number of genera, the first metasomatic tergum is more or less enlarged into a hornlike protuberance that houses the ovipositor when it is not in use. The species of this family are very common, and the greatest diversity of adults can be collected in spring and late summer when the eggs of their hosts are available.

***Family* Platygastridae:** The Platygastridae are minute, usually shining, black insects with very reduced wing venation (Figure 28–19H). In many cases the wings are completely veinless. The antennae usually have 10 segments and are attached very low on the face, next to the clypeus (Figure 28–22B). Most platygastrids are parasites of the larvae of Cecidomyiidae. *Platygaster hiemalis* Forbes is an important agent in control of the Hessian fly. Others attack mealybugs and other Sternorrhyncha (Hemiptera). Polyembryony occurs in several species in this family, with as many as 18 young developing from a single egg. Several groups, particularly the genus *Inostemma* have a horn formed from the first metasomatic tergum as in scelionids (Figure 28–61B). In some species, this horn extends far over the mesosoma and its apex fits into a notch in the posterior part of the head. In others, such as the genus *Synopeas*, the second metasomatic sternum is enlarged into a pouch or hornlike structure within which the elongate ovipositor is withdrawn when not in use (Figure 28–61A).

***Family* Chrysididae—Cuckoo Wasps:** The cuckoo wasps are small insects, rarely over 12 mm long, that are metallic blue or green. The body is usually coarsely sculptured. Some chalcidoids and bees are similar in size and color, but the cuckoo wasps can be recognized by the wing venation (Figure 28–21B)—a fairly complete venation in the front wing but no closed cells in the hind wing—and the structure of the metasoma. In most species, the metasoma consists of only three or four visible segments and is hollowed out ventrally. When a cuckoo wasp is disturbed, it usually curls up in a ball. Most cuckoo wasps are external parasites of full-grown wasp or bee larvae. The species in the genus *Cleptes* attack sawfly larvae, and those in *Mesitiopterus* attack the eggs of walkingsticks.

***Family* Bethylidae:** The Bethylidae are small to medium-sized, usually dark-colored wasps. The females of many species are wingless and antlike in appearance. In a few species, both winged and wingless forms occur in each sex. These wasps are parasites of the larvae of Lepidoptera and Coleoptera. Several species attack moths or beetles that infest grain or flour. A few species sting people.

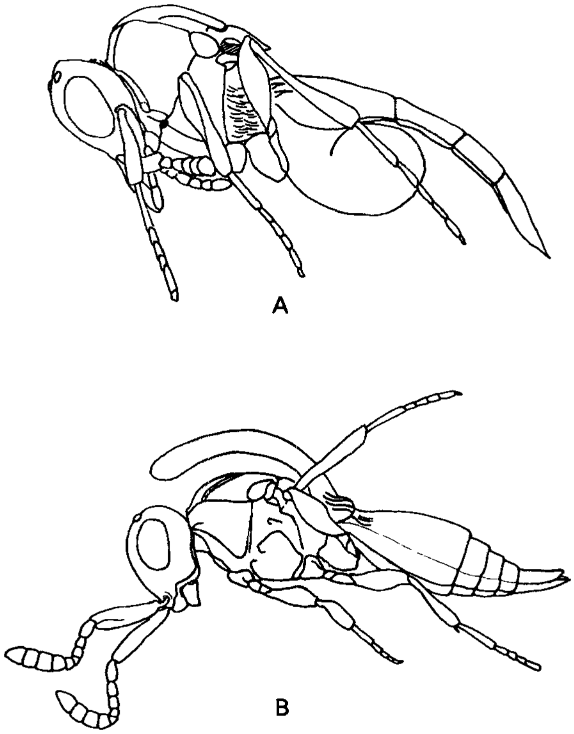

Figure 28–61 Platygastridae, illustrating some metasomatic modifications to accomodate the elongate ovipositor. A, *Synopeas*; B, *Inostemma*.

Family **Dryinidae:** The Dryinidae is a fairly small group (111 species in the Nearctic) of parasitoids of Hemiptera Auchenorrhyncha. The two sexes are often quite different in appearance, and the association can only be made clear by rearing them. Both males and females have 10-segmented antennae and are often characterized by their large heads and broad, strongly toothed mandibles. Most females are remarkable in that the fore tarsi are developed into chelae used for grasping and holding the hoppers used as hosts (Figure 28–30). Female dryinids catch an adult or host nymph with their chelae, sting and temporarily paralyze it, and lay an egg between two thoracic or abdominal segments. The parasitoid larva feeds internally on the host, although during most of its development a part of the larval body protrudes in a saclike structure. The parasite, when full -grown, leaves the host and spins a silken cocoon nearby. Polyembryony occurs in *Crovettia theliae* (Gahan), which attacks the treehopper *Thelia bimaculata* (Fabricius), with 40 to 60 young developing from a single egg. Many adult females are also predaceous on leafhoppers. Some dryinid females are remarkable ant mimics and may be associated with myrmecophilic hoppers.

Family **Embolemidae:** This small, rare family is sometimes classified with the dryinids. Both have 10-segmented antennae in both sexes. The antennae of embolemids arise from a frontal shelf similar to that in the family Diapriidae. Males are winged, females wingless. Two species of embolemids are known from North America. *Ampulicomorpha confusa* Ashmead has been reared from nymphs of Achilidae (Homoptera) feeding on fungi beneath the bark of fallen logs. Species of *Embolemus* (outside of North America) have been collected from ant nests that contain aphids or scale insects.

Family **Sclerogibbidae:** This family is represented in North America by a single, very rare species in Arizona, *Probethylus schwarzi* Ashmead. A few sclerogibbids (in other parts of the world) are known to be parasites of Embiidina.

SUPERFAMILY **Apoidea—Bees** and Sphecoid Wasps: Entomologists differ regarding the taxonomic arrangement of the sphecoid wasps and some of the names used for them. We follow here the arrangement of Bohart and Menke (1976), who put the sphecoids in a single family, the Sphecidae. The classification of bees is also a point of contention. At one extreme, some researchers place all bees in a single family, Apidae. We follow the classification of Michener (2000), in which the North American bees are classified in six families. Identification of bees to family is sometimes difficult because the characters are hidden beneath the dense body hairs or the tongue is folded beneath the head. The hairs can be carefully scraped off or pushed aside with an insect pin, and the tongue can be extended while the specimen is still fresh and flexible.

Bees are common insects and are found almost everywhere, particularly on flowers. About 3,500 species occur in North America. Many other species of Hymenoptera can be collected at flowers feeding on nectar. Bees are unusual in that they visit the flowers not only for the carbohydrates provided by the nectar, but also to collect the pollen produced by the plant with which to provision their nests. In most species the larvae feed and develop on a mass of pollen stored in the cell by the female bee, in contrast to other aculeates in which the cells are provisioned with arthropod prey (the Masarinae in the family Vespidae also provision their nests with pollen). Nests are typically constructed in the soil, but a wide variety of natural cavities may be used, such as abandoned rodent nests, tree hollows, the emergence holes of wood-boring beetles, or the hollow stems of plants. Some species of bees collect pollen from only a very narrow range of hosts; others may visit practically any plant in bloom. Most species are solitary; that is, each female is capable of constructing a nest and reproducing. These species construct a cell, completely provision it with pollen (mass provisioning), oviposit on or near the pollen, then close the cell and begin constructing another. The eusocial bees typically progressively provision the cells in their nest, bringing more pollen to the larvae as they grow or providing them with honey (collected in the form of nectar from flowers and concentrated by evaporation).

The bees are closely related to the Sphecidae, and their closest relatives are probably some subgroup of the sphecids. Together they form a distinctive group within the Hymenoptera. Their pronotum terminates laterally in rounded lobes that do not reach the tegulae. The distinctive features of the nonparasitic bees largely concern the transport of pollen (Figures 28–15B, 28–62). Most bees are quite hairy, and as they visit flowers, a certain amount of pollen sticks to their body hairs. This pollen is periodically combed off with the legs and transported on brushes of hairs called *scopae* (located on the ventral side of the metasoma in Megachilidae) or on corbiculae (the broad, shiny, slightly convex outer surfaces of the hind tibiae, Figure 28–15B, *cb*, as in the social Apidae). A few species transport pollen in their crop. The bees that are kleptoparasites, that is, those that live as "cuckoos" in the nests of other bees, are usually wasplike in appearance, with relatively little body hair and without a pollen-transporting apparatus. These can be recognized as bees by their more flattened hind basitarsi and the plumose body hairs.

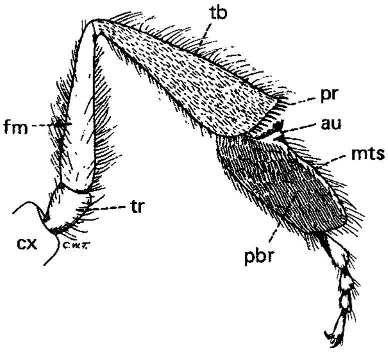

Figure 28–62 Hind leg of a honey bee, inner surface, showing the pollen-transporting apparatus. *au*, auricle; *cx*, coxa; *fm*, femur; *mts*, first tarsal segment; *pbr*, pollen brush; *pr*, pollen rake or pecten; *tb*, tibia; *tr*, trochanter. The pollen is collected off the body hairs by the front and middle legs and deposited on the pollen brushes (*pbr*) of the hind legs. The pollen on the pollen brush of one leg is raked off by the rake (*pr*) on the other, the pollen falling on the surface of the auricle (*au*); the closing of the tarsus on the tibia forces the pollen upward, where it adheres to the floor of the pollen basket or corbicula (which is on the outer surface of the tibia). As this process is repeated, first on one side and then on the other, the pollen is packed into the lower ends of the pollen baskets until both are filled.

The maxillae and labium of bees form a tonguelike structure through which the insect sucks up nectar. There is some development of such a tongue in other Hymenoptera, but in many bees the tongue is elongate, and the bee thus can reach the nectar in flowers with a deep corolla. The structure of the tongue differs considerably in different bees and provides characters that are used in classification.

The two sexes of bees differ in the number of antennal segments and metasomatic tergites. The males have 13 antennal segments and seven visible metasomatic tergites. The females have only 12 antennal segments and six visible metasomatic tergites.

The pollen-collecting bees play an important role in pollinating plants. Some higher plants are self-pollinating, but a great many are cross-pollinated; that is, the pollen of one flower must be transferred to the stigma of another. Cross-pollination is brought about by two principal agencies, wind and insects. Wind-pollinated plants include the grasses (such as the cereal grains, timothy, and the like), many trees (such as the willows, oaks, hickories, elms, poplars, and conifers), and many wild plants. The insect-pollinated plants include most orchard fruits, berries, many vegetables (particularly the cucurbits), field crops (such as the clovers, cotton, and tobacco), and flowers. Most pollination is done by bees—often chiefly honey bees and bumble bees, but a great deal of pollinating is done by solitary bees. Many growers, by bringing in hives of honey bees when the plants are in bloom, have been able to get greatly increased yields of orchard fruits, clover seed, and other crops that depend on bees for pollination. Given that the annual value of insect-pollinated crops in the United States is about $14.6 billion, clearly the bees are extremely valuable.

***Family* Sphecidae:** Sphecids can be distinguished from other wasps by the structure of the pronotum: In dorsal view the posterior margin is straight, and there is usually a constriction between it and the mesoscutum (forming a collar); laterally the pronotum terminates in a rounded lobe that does not reach the tegula. Most sphecids have a more or less vertical sulcus on the mesopleuron, the episternal sulcus. Such a sulcus is present in most vespoids, but the mesopleural sulcus in pompilids is transverse (Figure 28–34). In most sphecids, the inner margins of the eyes are not notched. This is also the case with the pompilids, but most vespoids do have notched inner margins of the eyes.

Sphecid wasps differ from the bees, which have a similar pronotal structure, in several ways: (1) All the body hairs are simple (some are branched or plumose in bees); (2) the basal segment of the hind tarsus is not particularly widened or flattened (as it is in most bees) and has at its base, on the inner side, a brush of hairs in a slight depression, opposed by a pectinate tibial spur; (3) sphecids are relatively bare, whereas many bees are quite hairy; and (4) the posterior margin of the pronotum in dorsal view is straight (usually slightly arcuate in bees). Most Sphecidae are moderate-sized to large, with a complete wing venation, but a few are quite small. Body length in this family varies from about 2 to more than 40 mm. Some of the very small sphecids have a much reduced wing venation, with only four or five closed cells in the front wing. Nine subfamilies are found in North America.

The members of this large family (more than 1,100 North American species) are solitary wasps, although large numbers may sometimes nest in a small area, and a few show the beginnings of social organization (a small number of tropical species are eusocial). They nest in a variety of situations. Most burrow in the ground, but some nest in various kinds of natural cavities (hollow plant stems, cavities in wood, and the like), and some construct nests of mud. Females hunt for arthropod prey that serves as food for their offspring. The prey is stung and paralyzed and then placed within the nest. In most cases the nest is completely provisioned before the egg is laid, but in some cases the female wasp continues to provide new prey items as her offspring grow (known as *progressive provisioning*). Some groups of sphecids are restricted to a particular type of prey as larval food, but a few groups vary considerably in their selection. A wide variety of arthropods are used, including Orthoptera, Blattodea, Hemiptera, Coleoptera, Diptera, Lepidoptera, Hymenoptera, and spiders. A few are kleptoparasitic, building no nest but laying their eggs in the nests of other wasps, their larvae feeding on the food stored for the host larvae.

The subfamily Sphecinae, or thread-waisted wasps, are very common insects, and most are 25 mm or more long. Some of the largest North American sphecids are in this subfamily. The common name refers to the very slender petiole of the metasoma. The two genera *Sceliphron* and *Chalybion* are commonly called "mud daubers." They construct nests of mud and provision them with spiders. These nests usually consist of a number of cells, each about 25 mm long, placed side by side. They are common on ceilings or walls of old buildings. Two species in each of these genera occur in the Nearctic, the most common being *S. caementarium* (Drury) and *C. californicum* (Saussure). The former is blackish brown with yellow spots, yellow legs, and clear wings, and the latter is metallic blue with bluish wings. Another common ground-nesting species of Sphecinae is *Sphex ichneumoneus* (L.), which is reddish brown with the tip of the metasoma black (Figure 28–63C).

The genus *Trypoxylon* (Crabroninae) includes the organ-pipe mud daubers (some of which reach a length of 25 mm or more), which make nests of mud (Figure 28–64). Other species of this common genus nest in the ground or in various natural cavities. These wasps provision their nests with spiders.

Many members of the Crabroninae (Figure 28–65) are small to medium-sized, rather stocky wasps. They are fairly common insects, and most are either black with yellow markings or entirely black. They can usually be recognized by the large, quadrate head, with the inner margins of the eyes straight and converging below, and the single submarginal cell. These wasps vary in their nesting habits. Most nest in the ground, but some nest in natural cavities such as hollow stems or cavities in wood. The principal prey is flies, but some take other insects such as beetles, bugs, hoppers, or small Hymenoptera.

The cicada killers (Nyssoninae: *Sphecius*) are large insects (up to 40 mm long) that provision their nests with cicadas. One common species, *S. speciosus* (Drury), is black or rusty, with yellow bands on the metasoma (Figure 28–66A).

The sand wasps (Nyssoninae) are rather stout-bodied wasps of moderate size (Figure 28–66B). This is a fairly large group (about 75 North American species), and its members are common around beaches, sand dunes, and other sandy areas. They nest in burrows, and a great many may nest in a small area. In some species, the adults continue to feed the larvae during their growth. The adults are very agile and rapid fliers, and although they can sting, one can walk through a colony—with the wasps dashing all about—without being stung. *Stictia carolina* (Fabricius), an insect about 25 mm long and black with yellow markings, is fairly common in the South. It often hunts for flies (mostly Tabanidae) near horses, and it is called the "horse guard." Other sand wasps are black with yellow, white, or pale green markings.

The species of the tribe Philanthini (Philanthinae; Figure 28–66C) provision their nests with bees, principally halictids, and are usually called "bee-killer wasps" or "bee wolves." They are common insects (29 North American species). The Cercerini (Philanthinae) (Figure 28–66D) may be called "weevil wasps," as they provision with beetles (Curculionidae, Chrysomelidae, and Buprestidae). They are common insects, and a little over a hundred species occur in North America.

***Family* Melittidae:** The melittids are small, dark-colored, rather rare bees, similar in nesting habits to the Andrenidae. They differ from other short-tongued bees (Colletidae, Halictidae, and Andrenidae) in that the jugal lobe of their hind wing is shorter than the $M+Cu_1$ cell. They differ from the Megachilidae and Apidae (the long-tongued bees) in that the segments of

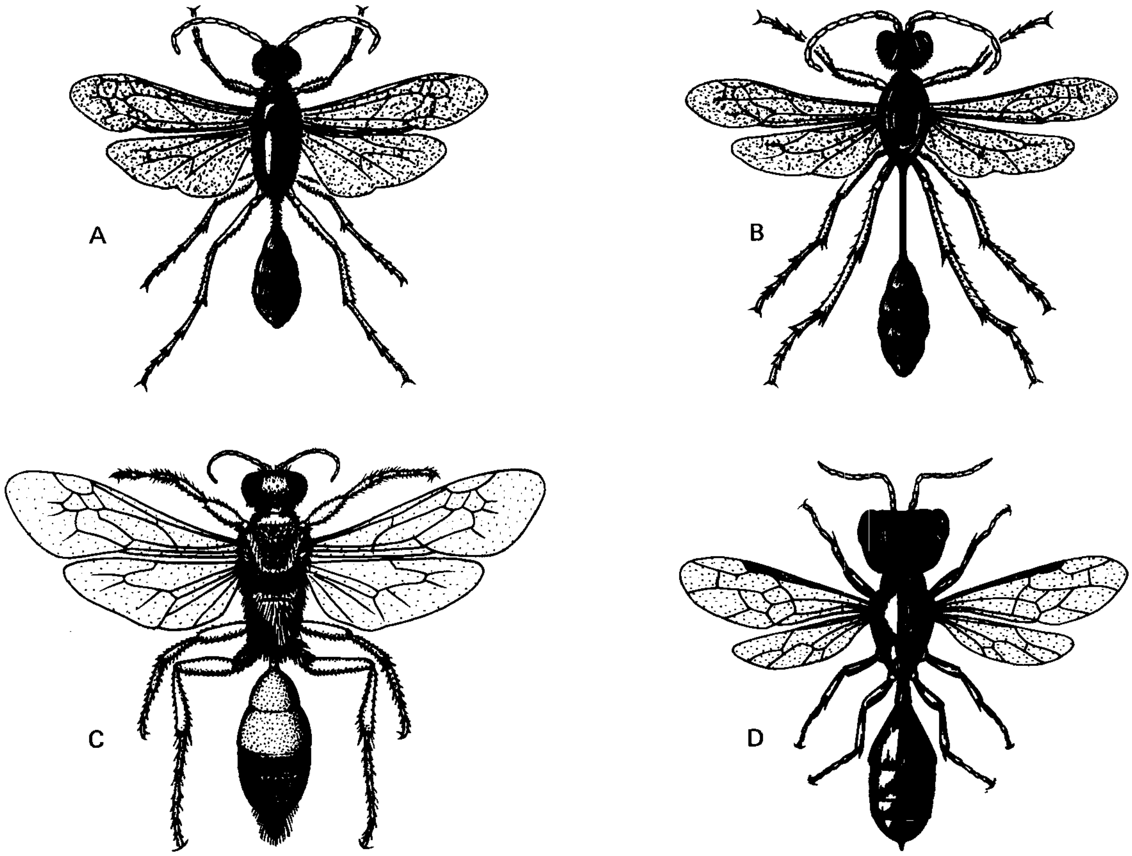

Figure 28–63 Sphecid wasps. A, *Chlorion aerarium* Patton; B, *Ammophila nigricans* Dahlbom; C, *Sphex ichneumoneus* (L.); D, *Pemphredon inornatus* Say.

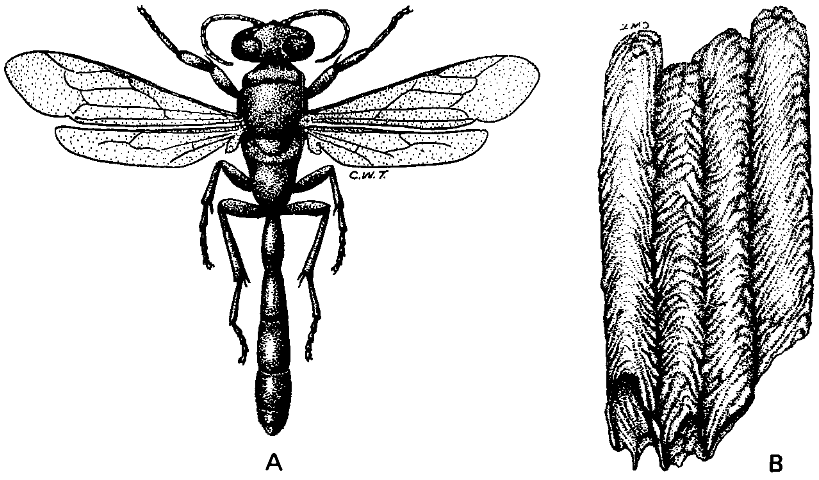

Figure 28–64 An organ-pipe mud dauber. A, adult of *Trypoxylon clavatum* Say, $3\frac{1}{2}\times$; B, nest of *T. politum* Say.

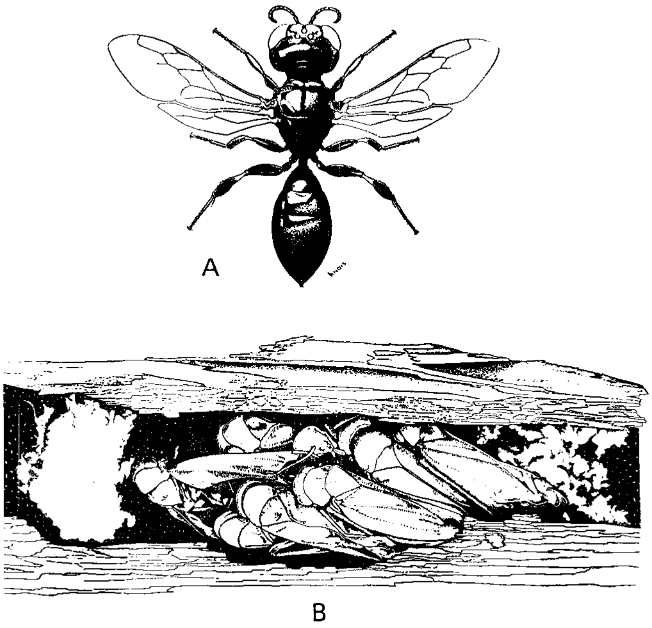

Figure 28–65 A square-headed wasp, *Crossocerus annulipes* (Lepeletier and Brullé) (Sphecidae, Crabroninae). A, adult, 2×; B, a section of a rotting log in which this wasp has stored leafhoppers. (Courtesy of Davidson and Landis and the Entomological Society of America.)

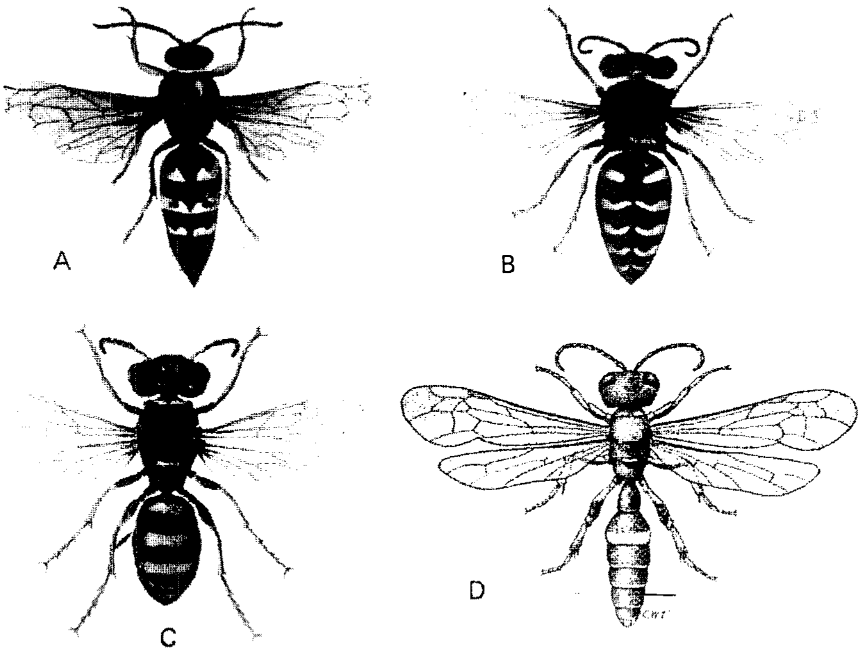

Figure 28–66 Sphecid wasps. A, the cicada-killer, *Sphecius speciosus* (Drury), about natural size; B, a sand wasp, *Bembix americanus spinolae* Lepeletier, slightly enlarged; C, a bee-killer wasp, *Philanthus ventilabris* Fabricius, 2×; D, a weevil wasp, *Cerceris clypeata* Dahlbom, 2×.

their labial palps are similar in size and cylindrical (the labial palps of the Megachilidae and Apidae have their first two segments elongate and flattened). The species nest in burrows in the soil.

Three subfamilies and 31 species of Melittidae occur in North America: the Macropidinae (with two submarginal cells and a very broad stigma), the Dasypodinae (with two submarginal cells and a narrow stigma), and the Melittinae (with three submarginal cells).

Family **Colletidae—Plasterer Bees and Yellow-Faced Bees:** These bees have the tongue short and either truncate or bilobed at the apex (Figure 28–6C). The family is divided into three subfamilies, the Colletinae, Diphaglossinae, and Hylaeinae, and more than 150 species are known from North America.

The Colletinae, or plasterer bees, burrow into the ground to nest and line their burrows with a thin, translucent substance. They are of moderate size and are quite hairy, with bands of pale pubescence on the metasoma. There are three submarginal cells, and the second m-cu crossvein is sigmoid (Figure 28–13D). Ninety-seven species of these bees have been recorded from North America. The Hylaeinae, or yellow-faced bees, are small, black, very sparsely hairy bees, usually with yellow markings on the face (Figure 28–67) and with only two submarginal cells (Figure 28–13E). They are very wasplike in appearance, and the hind legs of the female do not have pollen brushes. Pollen for larval food is carried to their nests in the crop, mixed with nectar, instead of on the body or legs. These bees nest in various sorts of cavities and crevices, in plant stems, or in burrows in the ground. North American species belong to the genus *Hylaeus*, and many are very common bees.

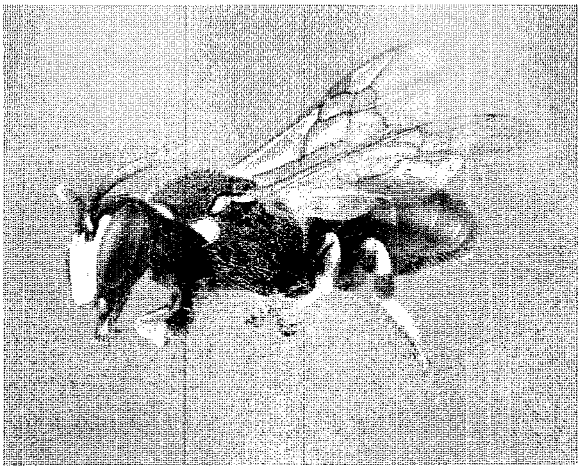
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Figure 28–67 A yellow-faced bee, *Hylaeus affinis* (Smith).

Family **Halictidae:** The halictids are small to moderate-sized bees, often metallic in color, and can usually be recognized by the strongly arched first free segment of the medial vein (Figure 28–13C). Most nest in burrows in the ground, either on level ground or in banks. The main tunnel is usually vertical, with lateral tunnels branching off from it and each terminating in a single cell. Large numbers of these bees often nest close together, and many bees may use the same passageway to the outside. More than 500 species of halictids occur in North America.

Three subfamilies of halictids occur in the United States: the Halictinae (the largest and most common of the three subfamilies), the Nomiinae, and the Rophitinae. The Rophitinae differ from the other two subfamilies in that they have only two submarginal cells and have a short clypeus, usually not longer than the labrum, and in profile strongly convex and protruding. The Nomiinae, represented by the genus *Nomia*, have the first and third submarginal cells about the same size. These bees are often of considerable importance in pollinating plants.

In the Halictinae, the third submarginal cell is shorter than the first. This group contains several genera of fairly common bees. In *Agapostemon* (Figure 28–68B), *Augochloropsis*, *Augochlorella*, and *Augochlora*, the head and mesosoma are a brilliant metallic green. These bees are small, 14 mm long or less, and some bees in the genus *Augochlora* are only a few millimeters long. The other fairly common genera are *Lasioglossum* and *Sphecodes*. Usually their head and mesosoma are black or dull green. Some members of the genus *Lasioglossum* are frequently attracted to people who are perspiring, and are called "sweat bees." The bees in the genus *Sphecodes* are rather wasplike in appearance, and the entire metasoma is red. These are parasites (kleptoparasites) of other bees.

Halictids are extremely diverse in terms of their social biology, spanning the spectrum from solitary species, either nesting alone or in congregations, to primitively eusocial species. The level of social "development" seems to be intertwined with poorly understood environmental constraints: Some species show great differences in social behavior in different parts of their range or at different times of the year. Eusociality, per se, is clearly not an evolutionary goal toward which these bees are inevitably moving, but most likely represents an adaptive strategy for a particular time and place. Michener (1974), in fact, argues that it is quite likely that in addition to having evolved many times, eusociality may have been lost just as often by different species.

Family **Andrenidae:** The andrenids are small to medium-sized bees that can be recognized by the two subantennal sulci below each antennal socket (Figure 28–17A). They nest in burrows in the ground,

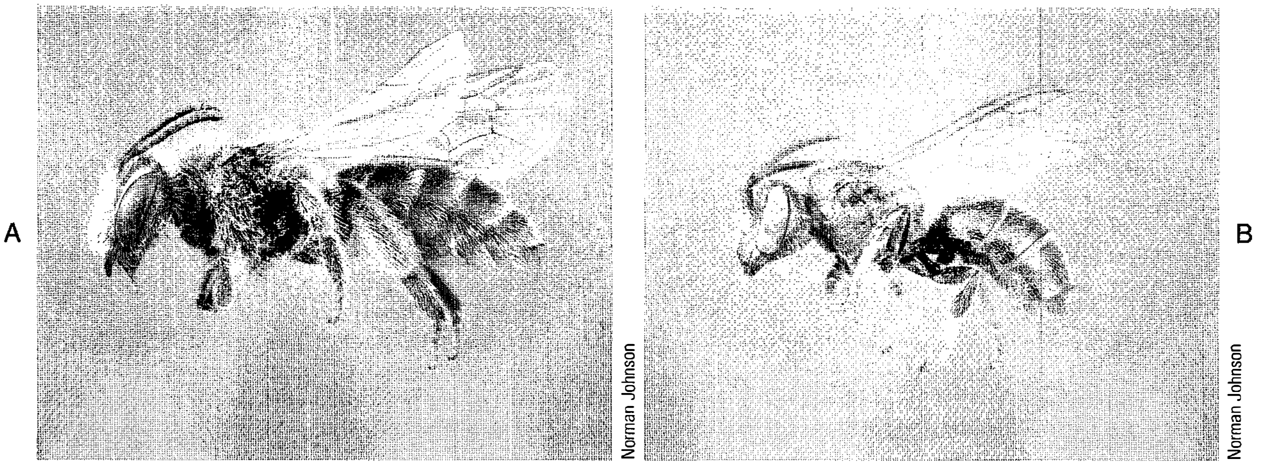

Figure 28–68 Solitary bees. A, *Andrena imitatrix* Cresson (Andrenidae); B, *Augochloropsis metallica* (Fabricius) (Halictidae).

and their burrows are similar to those of halictids. Sometimes large numbers of these bees nest close together, usually in areas where the vegetation is sparse.

The approximately 1,200 species of andrenids in North America are arranged in three subfamilies, the Andreninae, Oxaeinae, and the Panurginae. The Andreninae have the apex of the marginal cell pointed or narrowly rounded and on the costal margin of the wing, and they usually have three submarginal cells (Figure 28–13A). The Panurginae have a truncate apex of the marginal cell and usually have only two submarginal cells (Figure 28–13B). The vast majority of species of Andreninae belong to the genus *Andrena* (Figure 28–68A), which are very common springtime bees. Most Panurginae belong to the genus *Perdita*. The Panurginae are moderate-sized to minute, and many have yellow or other bright markings. The Oxaeinae are chiefly tropical and are represented in the United States by two species each in the genera *Protoxaea* and *Mesoxaea* that occur in the Southwest. These solitary bees are large and fast-flying and nest in deep burrows in the soil.

***Family* Megachilidae—Leaf-Cutting Bees**: The leaf-cutting bees are mostly moderate-sized, fairly stout-bodied bees (Figure 28–69). They differ from most other bees in having two submarginal cells of about equal length (Figure 28–13F), and the females of the pollen-collecting species carry the pollen by means of a scopa on the ventral side of the metasoma rather than on the hind legs. The common name of these bees is derived from the fact that in many species the nest cells are lined with pieces cut from leaves. These pieces are usually very neatly cut out, and it is not uncommon to find plants from which these bees have cut circular pieces. A few species in this family are parasitic. The nests are made in various places, occasionally in the ground but more often in some natural cavity, frequently in wood. The vast majority of nonparasitic species are solitary.

This family is represented in North America only by the subfamily Megachilinae. This is a large group (more than 600 North American species) of widespread distribution. Some of the more common genera of Megachilinae are *Anthidium, Dianthidium, Stelis, Heriades, Hoplitis, Osmia, Megachile,* and *Coelioxys*. The bees in the genera *Stelis* and *Coelioxys* are parasitic. One introduced species of *Megachile* is an important pollinator of alfalfa in the West.

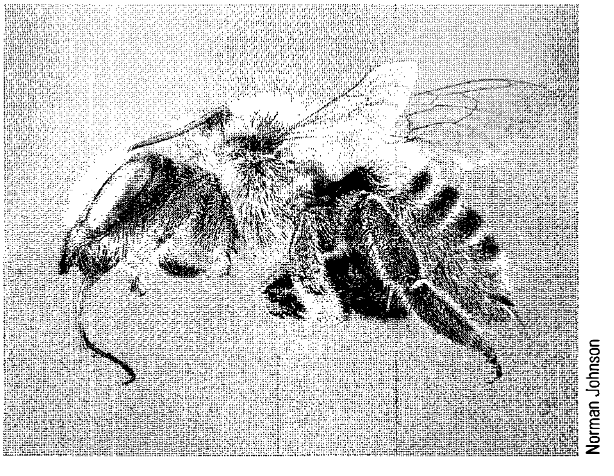

Figure 28–69 A leaf-cutting bee, *Megachile latimanus* Say.

Figure 28–70 Nest of the small carpenter bee, *Ceratina dupla* Say.

Family **Apidae—Cuckoo Bees, Digger Bees, Carpenter Bees, Bumble Bees, Orchid Bees, Stingless Bees, Honey Bees:** Until recently, the cuckoo bees, digger bees, and carpenter bees were placed in the family Anthophoridae. The North American species of these long-tongued bees are divided into three subfamilies: the Nomadinae, the Xylocopinae, and the Apinae.

Subfamily **Xylocopinae—Carpenter Bees:** These bees do not have a protuberant clypeus, the front coxae are transverse, and the last metasomatic segment lacks a triangular, platelike area. These bees make their nests in wood or plant stems. The two North American genera in this group, *Ceratina* and *Xylocopa*, differ somewhat in habits and differ considerably in size. The small carpenter bees (*Ceratina*) are dark bluish green and about 6 mm long. They are superficially similar to some of the halictids, particularly because the first free segment of the medial vein is noticeably arched, but they can be distinguished from a halictid by the much smaller jugal lobe in the hind wings (compare Figures 28–13C and 28–14F). These bees excavate the pith from the stems of various bushes and nest in the tunnels so produced (Figure 28–70). The large carpenter bees (*Xylocopa*) are robust bees about 25 mm long, similar in appearance to bumble bees, but the dorsum of their metasoma is largely bare (Figure 28–71A), and the second submarginal cell is triangular (Figure 28–14A). These bees excavate galleries in solid wood.

Subfamily **Nomadinae—Cuckoo Bees:** All the bees in this group are parasites in the nests of other bees. They are usually wasplike in appearance and have relatively few hairs on the body. They lack a pollen-transporting apparatus, the clypeus is somewhat protuberant, the front coxae are a little broader than long, and the last metasomatic tergite usually (at least in females) has a triangular, platelike area. Some of these bees (for example, members of the large genus *Nomada*) are reddish and of medium or small size. Others (for example, *Epeolus* and *Doeringiella*, Figure 28–72)

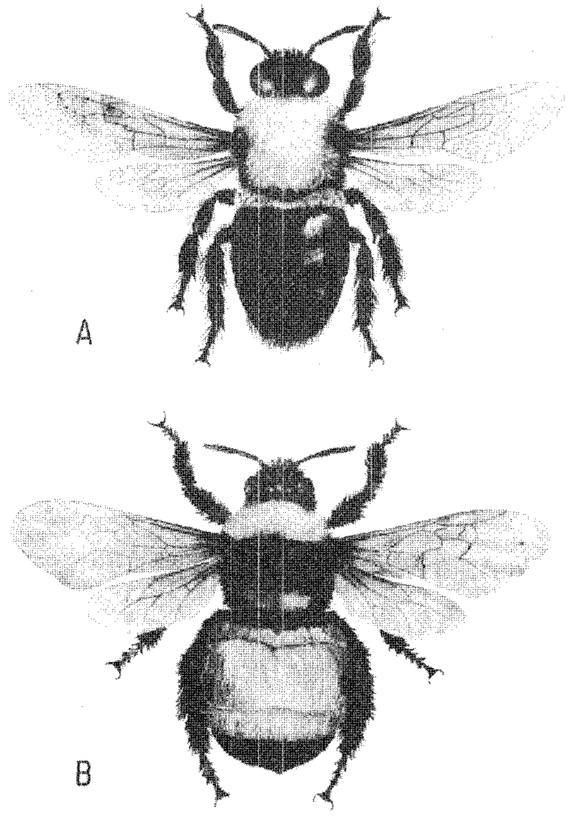

Figure 28–71 A, a large carpenter bee, *Xylocopa virginica* (L.) (Xylocopinae); **B**, a bumble bee, *Bombus pensylvanicus* (DeGeer) (Apinae). 1½×.

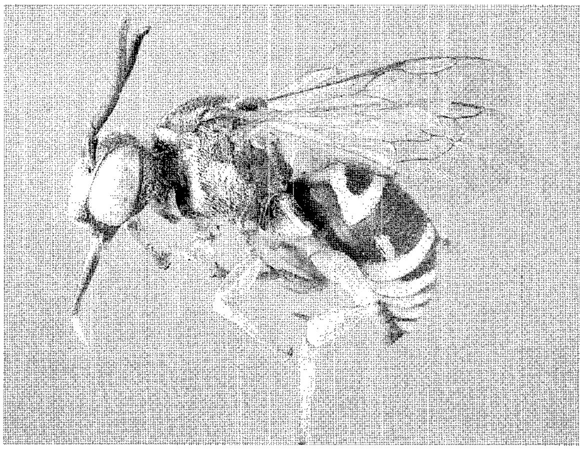

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Figure 28–72 A cuckoo bee, *Doeringiella lunata* (Say) (Apidae).

are fair-sized (13–19 mm) and dark-colored, with small patches of pale pubescence.

Subfamily Apinae—Digger Bees, Bumble Bees, Honey Bees, and Orchid Bees: The digger bees resemble the Nomadinae in the form of the clypeus, front coxae, and the tergal plate on the last metasomatic segment, but are robust and hairy (Figure 28–73A). The subfamily includes both parasitic and nonparasitic species. Most of the latter are solitary, but some nest communally. Digger bees nest in burrows in the ground or in banks, and the cells are lined with a thin wax or varnishlike substance.

Bumble bees can usually be recognized by their robust shape and black-and-yellow coloration (Figure 28–71B); a few are marked with orange or white. They are relatively large bees, most being 20 mm or more long. The hind wings lack a jugal lobe (Figure 28–14B). Bumble bees are very common insects, and they are important pollinators of certain kinds of clover because of their very long tongues.

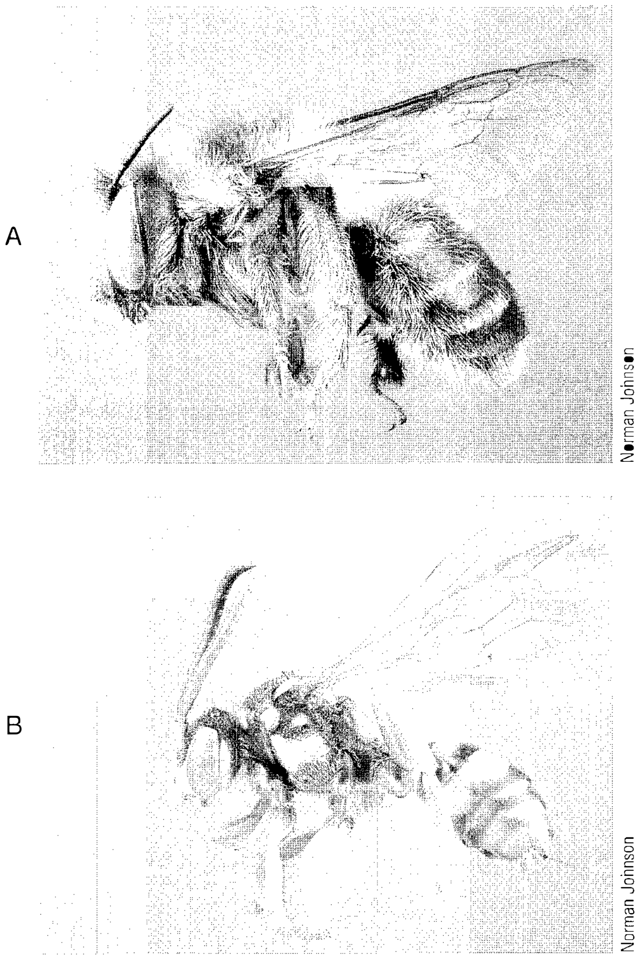

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Figure 28–73 A, a digger bee, *Anthophora terminalis* Cresson; B, a cuckoo bee, *Nomada*.

Most bumble bees nest in the ground, usually in a deserted mouse nest or bird nest or similar situation. The colonies are annual (at least in temperate regions), and only the fertilized queens overwinter. Nests are initiated by solitary, fertilized queens that have overwintered. These queens are often very conspicuous in the spring as they search for a nest site. The first brood raised by the queen consists entirely of workers. Once the workers appear, they take over all the duties of the colony except egg laying. They enlarge the nest, collect food, and store it in saclike "honey pots" built from wax and pollen, and care for the larvae. Later in the summer, males and queens are produced, and in the fall all but these queens die.

Some species of *Bombus* are parasites of other bumble bees, and some entomologists place them in the genus *Psithyrus*. The parasitic females differ from those of other *Bombus* in having the outer surface of the hind tibiae convex and hairy (usually flat or concave and largely bare). These bees have no worker caste. The females invade the nests of other bumble bees and lay their eggs, leaving their young to be reared by the workers of the host nest.

The orchid bees are brilliant metallic, often brightly colored bees that are tropical in distribution. They have a very long tongue, they have apical spurs on the hind tibiae, they lack a jugal lobe in the hind wings, and the scutellum is produced backward over the metasoma. The common name arises because the males are attracted to orchid flowers and are important in their pollination. The males do not feed on this pollen and the orchids do not produce nectar; researchers think that the males may derive precursor chemicals for a sex pheromone from the flowers. Females are not attracted to orchids. Both parasitic and nonparasitic species are found in the subfamily. The latter include solitary and parasocial species. One species in this group, *Eulaema polychroma* (Mocsáry), has been recorded from Brownsville, Texas.

Honey bees can be recognized by their golden brown coloration and characteristic shape (Figure 28–74), the form of the marginal and submarginal cells in the front wing (Figure 28–14D), and the absence of spurs on the hind tibiae. These bees are common and well-known insects, and they are the most important bees in plant pollination. They are extremely valuable, as they produce some $300 million worth of honey and beeswax annually, and their pollinating activities are worth 130 to 140 times this amount.

Only a single species of honey bee occurs in North America, *Apis mellifera* L. This is an introduced species, and most of its colonies are in human-made


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Figure 28–74 The honey bee, *Apis mellifera* L., 5×.

hives. Escaped swarms usually nest in a hollow tree. The cells in the nest are in vertical combs, two cell layers thick. Honey bee colonies are perennial, with the queen and workers overwintering in the hive. A queen may live several years. Unlike the bumble bee queen, a honey bee queen cannot start a colony by herself. As in most Hymenoptera, the sex of a bee is in large part controlled by the fertilization of the egg: Fertilized eggs develop into females, and unfertilized eggs develop into males. Whether a larval honey bee destined to become a female becomes a worker or queen depends on the sort of food it is fed. There is normally only one queen in a honey bee colony. When a new one is produced, it may be killed by the old queen, or one of the queens (usually the old queen) may leave the hive in a swarm, along with a group of workers, and build a nest elsewhere. The new queen mates during a mating flight and thereafter never leaves the nest except to swarm. The males serve only to fertilize the queen and die in the act of mating. They do not remain in the colony long, as they are eventually killed by the workers.

North American honey bees, which have been introduced into this continent from Europe, are not particularly aggressive and are easy to manage. In 1956 an African strain of the honey bee was brought into southern Brazil with the intention of interbreeding them with the European strain. Mated queens and workers accidentally escaped and established wild colonies. This strain of the bee has become known as the "killer bee." Since its introduction this strain has spread over a large part of South and Central America, and into the southern United States. These bees produce more honey than the European strain, but they are very aggressive. At the slightest disturbance they attack people or animals with great ferocity, often chasing them 100 to 200 meters (sometimes as far as a kilometer). Both livestock and people have been killed by these bees. Beekeeping practices in South America have changed somewhat as a result of the introduction of this strain: Colonies are now generally removed from settlements and livestock. Attempts are being made to reduce the aggressiveness of these bees by crossbreeding and selection.

Honey bees have a very interesting "language," a means of communicating with one another (see von Frisch 1967, 1971). When a worker goes out and discovers a flower with a good nectar flow, she returns to the hive and "tells" the other workers about it—the type of flower, its direction from the hive, and how far away it is. The type of flower involved is communicated by means of its odor, either on the body hairs of the returning bee or in the nectar it brings back from the flower. The distance and direction of the flower from the hive are "told" by means of a dance put on by the returning worker. Many social insects have a "language" or a means of communication, but its exact nature is known in relatively few species.

***Family* Tiphiidae:** Most tiphiids are easily recognized by the platelike lamellae that extend over the bases of the middle coxae. The Tiphiinae is the largest subfamily, with about 140 North American species, and its members are fairly common and widely distributed. They are black, mostly medium-sized, and somewhat hairy, with short, spiny legs (Figure 28–75A). The larvae are parasites of scarab beetle larvae. One species, *Tiphia popilliavora* Rohwer (Figure 28–75A), has been introduced into the United States to help control the Japanese beetle. The Myzininae are generally a little larger (length up to about 25 mm) and more slender than the Tiphiinae and are black with yellow markings. The upcurved spine at the end of the male metasoma looks like a vicious sting, but is not dangerous. Fourteen species occur in the United States and Canada, and some are fairly common. These wasps are parasites of the larvae of scarab beetles. The Brachycistidinae are medium-sized, brownish, somewhat hairy wasps that are common throughout the West. The females are wingless and are not seen as often as the males. About 70 species occur in North America, but little is known of their immature stages. The Anthoboscinae is represented by a single species, *Lalapa lusa* Pate, which occurs in Idaho and California. Nothing is known of its immature stages. The Methochinae are small, usually

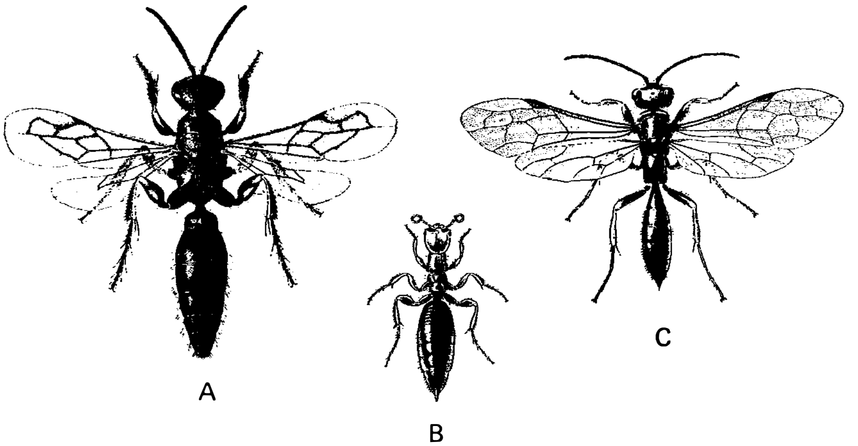


Figure 28–75 Tiphiid wasps. A, *Tiphia popilliavora* Rohwer, male (Tiphiinae); B, *Neozeloboria proximus* Turner, female (Brachycistidinae); C, same, male. (A, courtesy of USDA; B and C, courtesy of Burrell and the New York Entomological Society.)

black wasps, in which the females are wingless and generally much smaller than the males. Five species occur in the United States and Canada, and they are widely distributed but uncommon. The Methochinae are parasites of the larvae of tiger beetles.

Family **Sierolomorphidae:** The Sierolomorphidae are a small (six North American species) but widely distributed group of shining, black wasps 4.5 to 6.0 mm long. They are quite rare, and nothing is known of their immature stages.

Family **Sapygidae:** The Sapygidae are a small (17 North American species) and rare group. The adults are of moderate size, usually black spotted or banded with yellow, and with short legs. They are parasites of leaf-cutting bees (Megachilidae) and wasps.

Family **Mutillidae—Velvet Ants:** These wasps are called "velvet ants" because the females are wingless and antlike and are covered with a dense pubescence (Figure 28–76). In most mutillid females, the mesosomatic segments are completely fused to form an immovable boxlike structure (in the subfamily Myrmosinae, the pronotal and mesonotal suture is movable). The males are winged and usually larger than the females and are also densely pubescent. Most species have "felt lines" laterally on the second metasomatic tergum. Felt lines are narrow longitudinal bands of relatively dense, closely appressed hairs. The females have a very painful sting. Some species can stridulate, and they produce a squeaking sound when disturbed. Most mutillids whose life histories are known are external parasites of the larvae and pupae of various wasps and bees. A few attack beetles and flies. Mutillids are generally found in open areas. This group is a large one (about 435 North American species), and most species occur in the South and West, especially in arid areas.

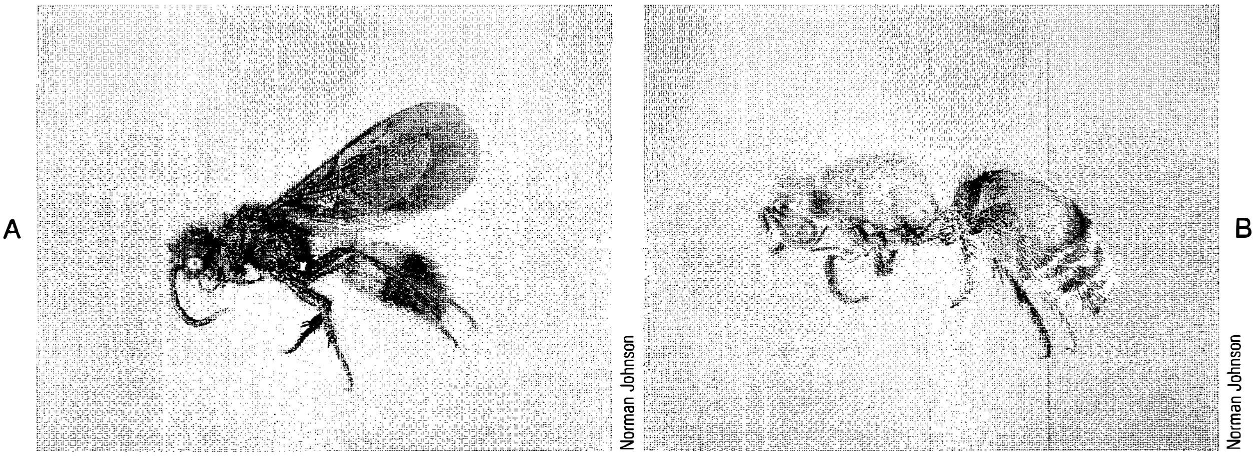


Figure 28–76 A velvet ant, *Dasymutilla nigripes* (Fabricius). A, male; B, female.

Family **Bradynobaenidae:** The bradynobaenids were formerly classified in the family Mutillidae because many of them have the lateral felt lines on the second metasomatic tergum. The males are winged and the females apterous. The males are distinguished from the mutillids by the presence of a jugal lobe in the hind wing. The females have a flexible articulation between the pronotum and mesonotum. Forty-eight species are found in western North America. The subfamily Typhoctinae is nocturnal, the Chyphotinae are diurnal. Their hosts and larval biology are unknown.

Family **Pompilidae—Spider Wasps:** The pompilids are slender wasps with long, spiny legs, a pronotum that is somewhat quadrate in lateral view, and a characteristic transverse sulcus across the mesopleuron (Figures 28–34, 28–77). The more common members of this group are 15–25 mm long, but some western species are 35–40 mm long. Most spider wasps are dark-colored, with smoky or yellowish wings. A few are brightly colored. They are often recognizable because of their habit of nervously flitting the wings while searching on foot. (There are a number of pompilid mimics, for example in the Sphecidae and Ichneumonidae, that also have this habit.) The adults are usually found on flowers or on the ground in search of prey. The larvae of most species feed on spiders (hence the common name), although these are not the only wasps that attack spiders. The spider wasps generally capture and paralyze a spider and then prepare a cell for it in the ground, in rotten wood, or in a suitable crevice in rocks. Some spider wasps construct a cell first, then hunt for a spider to store in the cell. A few species attack the spider in its own cell or burrow and do not move it after stinging and ovipositing on it. A few species oviposit on spiders that have been stung by another wasp. The spider wasps are fairly common (290 North American species), and the females have a very painful sting.

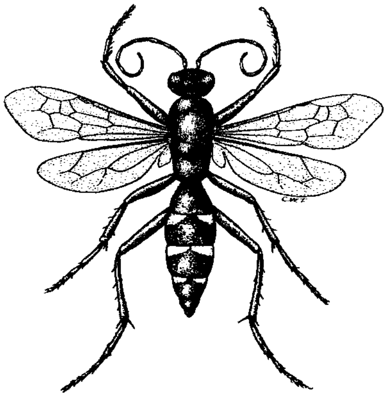


Figure 28–77 A spider wasp, *Episyron quinquenotatus* (Say), 2½×.

Family **Rhopalosomatidae:** This group includes three rare species that occur in the East, *Rhopalosoma nearcticum* Brues, *Liosphex varius* Townes, and *Olixon banksii* (Brues). *Rhopalosoma nearcticum* is 14–20 mm or more long, is light brown, and superficially resembles ichneumonids in the genus *Ophion*, but it does not have the metasoma compressed, the antennae contain only 12 (female) or 13 (male) segments, and there is only one m-cu crossvein in the front wing (Figure 28–31H). *Olixon banksii* is about 6 mm long and has greatly reduced wings that extend only to the tip of the propodeum. The larvae of these wasps attack crickets.

Family **Scoliidae:** The Scoliidae are large, hairy, and usually black with a yellow band (or bands) on the metasoma (Figure 28–78). Larvae of these wasps are external parasites of the larvae of scarabaeid beetles. The adults are commonly found on flowers. The females burrow into the ground to locate a host. When they find a grub, they sting it and paralyze it, then burrow deeper into the soil and construct a cell around the grub. Many grubs may be stung without the wasp ovipositing. Such grubs usually do not recover. Twenty-three species have been recorded in North America.

Family **Vespidae—Paper Wasps, Yellow Jackets, Hornets, Mason Wasps, Potter Wasps:** This is a relatively large group (325 North American species), and its members are very common and well-known insects. Most are black with yellow or whitish markings (Figure 28–80) or brownish (Figure 28–82A). Some species are eusocial, and the individuals in a colony are of three castes: queens, workers, and males. The queens and workers have a very effective sting. In some species there is very little difference between the queens and workers, but usually the queen is larger.

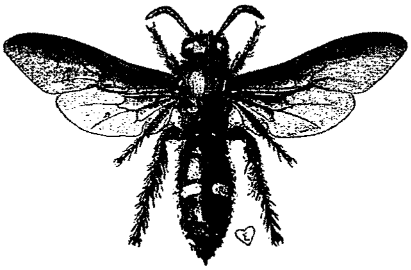


Figure 28–78 *Scolia dubia* Say (Scoliidae), a parasite of the green june beetle. (Courtesy of Davis and Luginbill and the North Carolina Agricultural Experiment Station.)

The social vespids construct a nest out of a papery material that consists of wood or foliage chewed up and elaborated by the insect. The colonies in temperate regions exist for just a single season. Only the queens overwinter, and in the spring each queen starts a new colony. The queen begins construction of a nest (or she may use a nest built in a previous year) and raises her first brood, which consists of workers. The workers then assume the duties of the colony, and thenceforth the queen does little more than lay eggs. The larvae are fed chiefly on insects and other animals.

Subfamily Euparagiinae: This small and rare group of vespids is found only in the western United States. The subfamily contains only one genus, *Euparagia*, with six described Nearctic species. This is the sister group of all other species in the Vespidae, and it is unique among them in that these insects do not fold the wings longitudinally at rest. One species, *E. scutellaris* Cresson, builds a shallow nest in the soil and provisions its cells with weevil larvae.

Subfamily Masarinae: The members of this subfamily are limited to the western United States. Most members of this group are black and yellow wasps, 10–20 mm long. They differ from other vespids in having only two submarginal cells and in having clubbed antennae. They make nests of mud or sand attached to rocks or twigs and provision their nests with pollen and nectar. This group is a small one, with only 21 species (14 in the genus *Pseudomasaris*) in North America.

Subfamily Eumeninae—Mason and Potter Wasps: These are solitary wasps and, in terms of numbers of species, the most abundant vespids (260 species in North America). They vary considerably in their nesting habits, but most provision their nests with caterpillars. Some species use cavities in twigs or logs for a nest, others burrow in the ground, and others make a nest of mud or clay (Figure 28–79B). Most are black marked with yellow or white, or entirely black, and they vary in length from about 10 to 25 mm.

Subfamily Vespinae—Yellow Jackets and Hornets: Most of the 18 North American species of Vespinae belong to the genus *Vespula* (Figure 28–80B). These wasps are eusocial, and their nests consist of several to many tiers of hexagonal paper cells, all enclosed in a papery envelope (Figure 28–81). Some species build their nests in the open, attached to branches, under a porch, or beneath any projecting surface. Other species build their nests in the ground. The most common exposed nests, some of which may be nearly 0.3 m in diameter, are made by the bald-faced hornet, *Dolichovespula maculata* (L.), an insect that is largely black with yellowish white markings (Figure 28–80A). Most yellow jackets (Figure 28–80B) nest in the ground.

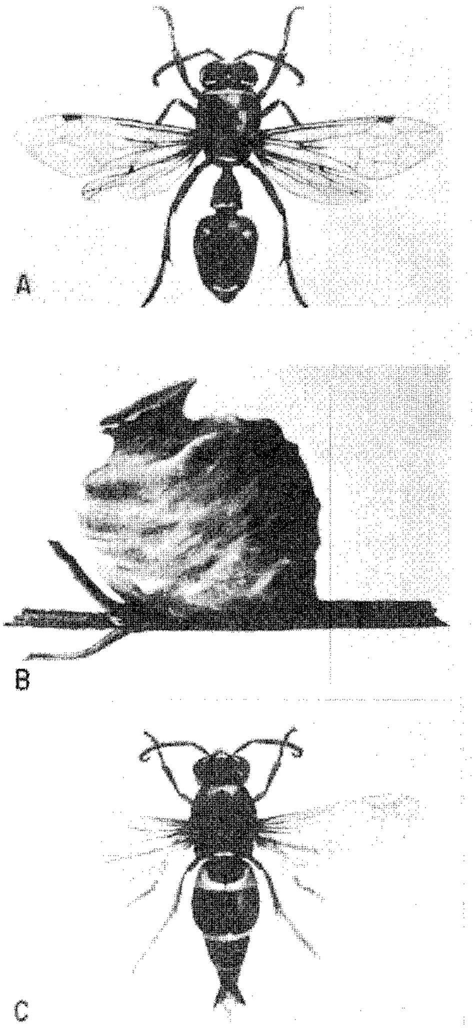


Figure 28–79 A, adult, and B, nest, of a potter wasp, *Eumenes fraternus* Say; C, a mason wasp, *Rygchium dorsale* (Fabricius); this species nests in small colonies in vertical burrows in the ground.

Subfamily Polistinae—Paper Wasps: The Polistinae are elongate and slender, with a spindle-shaped metasoma, and are usually reddish or brown marked with yellow (Figure 28–82). They are primitively eusocial; colonies may be started by individuals or by a small group of females. Their nests (Figure 28–82B) consist of a single, more-or-less circular, horizontal comb of paper cells, suspended from a support by a slender stalk. The cells are open on the lower side while the larvae are growing, and are sealed when the larvae pupate. The most common North American species in this subfamily belong to the genus *Polistes* (17 species). In addition, two species of *Mischocyttarus* occur in the southern and western United States, one species of

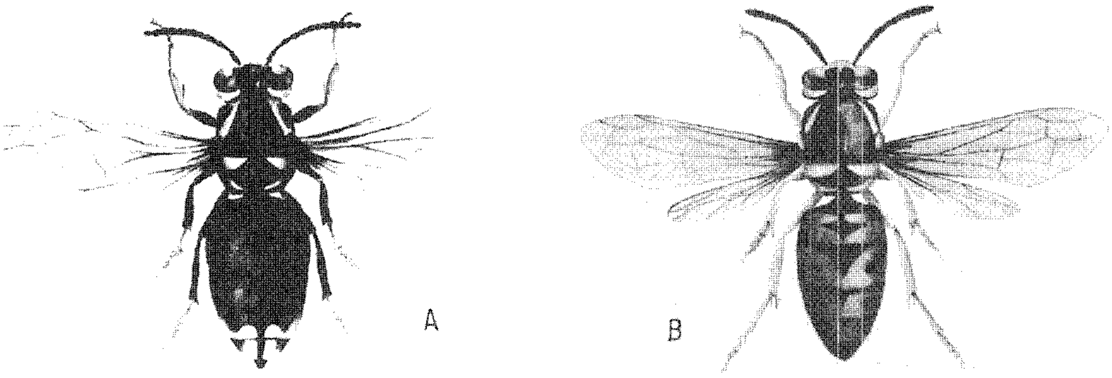


Figure 28–80 Vespinae. A, the bald-faced hornet, *Dolichovespula maculata* (L.); B, a yellow jacket, *Vespula maculifrons* (Buysson).

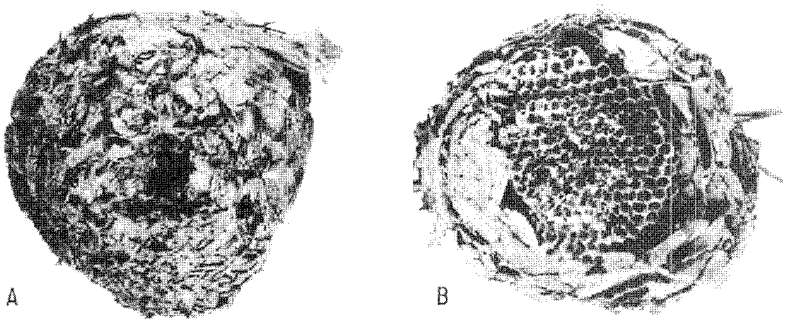


Figure 28–81 Nests of the bald-faced hornet, *Dolichovespula maculata* (L.). A, a nest as seen from below, showing entrance opening; B, a nest with the lower part of the outer envelope removed to show a tier of cells.

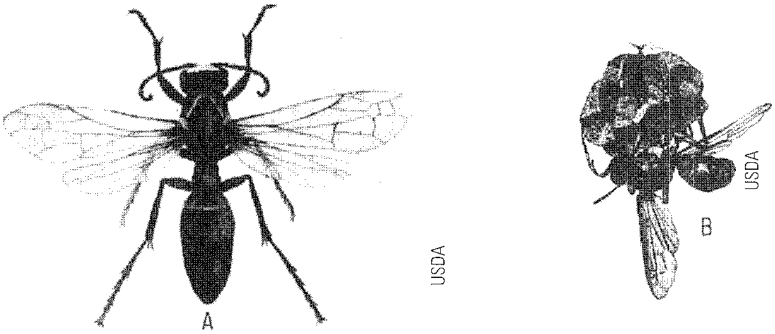


Figure 28–82 A paper wasp, *Polistes fuscatus* Fabricius. A, adult female; B, adult at nest.

Brachygastra occurs in southern Texas and southern Arizona, and two species of *Polybia* have been recorded from Nogales, Arizona.

***Family* Formicidae—Ants:** This is a very common and widespread group, well known to everyone. The ants are probably the most successful of all the insect groups. They occur practically everywhere in terrestrial habitats and outnumber in individuals most other terrestrial animals. The habits of ants are often very elaborate, and a great many studies have been made of ant behavior.

Although most ants are easily recognized, a few other insects strongly resemble and mimic ants, and some winged forms of ants resemble wasps (from which they are derived). One distinctive structural feature of ants is the form of the pedicel of the metasoma, which is one- or two-segmented and bears an upright lobe (Figures 28–11, 28–83). The antennae are usually elbowed (the males may have the antennae filiform), and the first segment is often very long.

All ants are basically eusocial insects (some parasitic species occur), and most colonies contain at least three castes: queens, males, and workers (Figure 28–83). The queens are larger than the members of the other castes and are usually winged, though the wings are shed after the mating flight. The queen usually starts a colony and does most of the egg laying in the colony. The males are winged and usually considerably smaller than the queens. They are short-lived and die soon after mating. The workers are sterile wingless females that make up the bulk of the colony. In the smaller ant colonies, there are usually just the three types of individuals, but in many of the larger colonies there may be two or three types within the worker caste. These may vary in size, shape, or behavior.

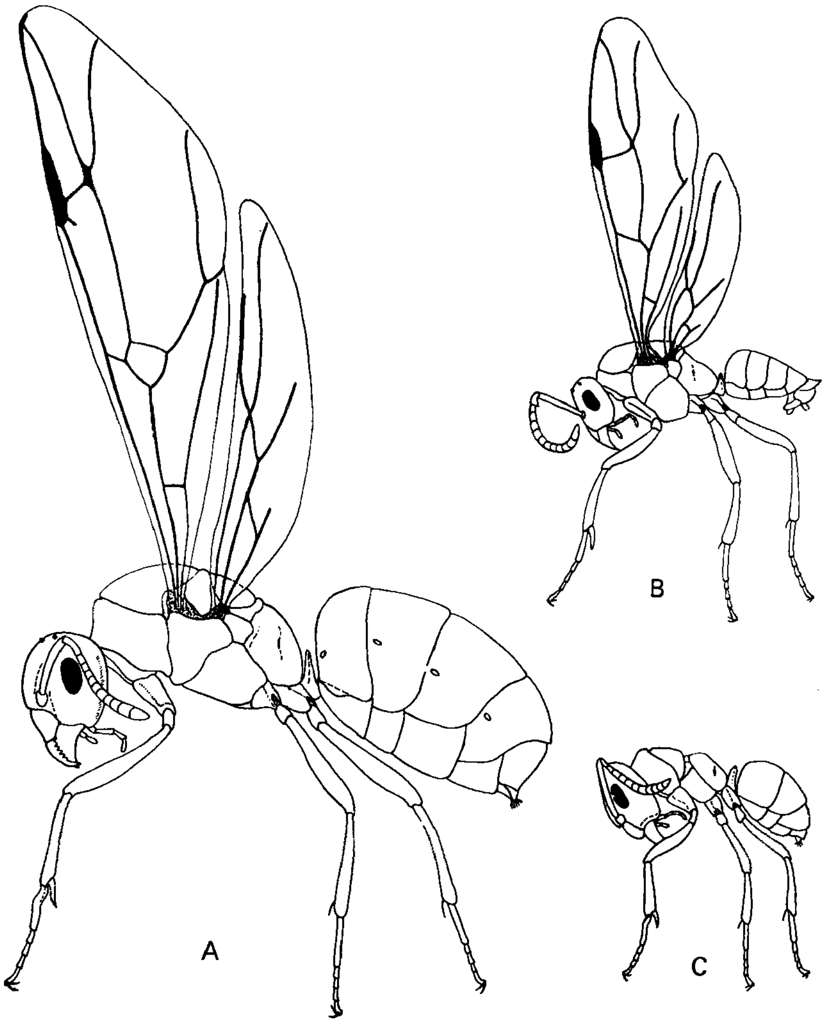


Figure 28–83 Castes of an ant (*Formica* sp.). A, queen; B, male; C, worker.

Ant colonies vary greatly in size, from a dozen or more up to many thousands of individuals. Ants nest in all sorts of places. Some nest in cavities in plants (in stems, in nuts or acorns, in galls, and so on); some (for example, the carpenter ants) excavate galleries in wood; but perhaps the majority of ants in North America nest in the ground. The ground nests of ants may be small and relatively simple, or they may be quite large and elaborate, consisting of a maze of tunnels and galleries. The galleries of some of the larger ground nests may extend several meters underground. Certain chambers in such underground nests may serve as brood chambers, others as chambers for the storage of food. Most ants shift their brood from one part of the nest to another as environmental conditions change.

Males and queens in most ant colonies are produced in large numbers only at one time of the year, when they emerge and engage in mating flights. Shortly after mating, the males die. The queen sheds her wings immediately after the mating flight, locates a suitable nesting site, makes a small excavation, and produces her first brood. This first brood, consisting of workers, is fed and cared for by the queen. Once the first workers appear, they take over the work of the colony—nest construction, caring for the young, gathering food, and the like—and henceforth the queen does little more than lay eggs. The queens of some species may live for several years. There may be more than one queen in some colonies. In some species of ants, certain castes or types of individuals may not be produced until the colony is several years old. In some species, the queen goes into an already established colony. This established colony may be of her own or of an alien species. In the latter case, her offspring may be spoken of as "temporary" or "permanent social parasites," as the case may be.

The feeding habits of ants are rather varied. Many are carnivorous, feeding on the flesh of other animals (living or dead); some feed on plants; some feed on fungi; and many feed on sap, nectar, honeydew, and similar substances. Ants in the nest often feed on the secretions of other individuals, and the exchange of food between individuals (trophallaxis) is common.

Ants produce a number of exocrine secretions that function in offense, defense, and communication. These are emitted to the outside chiefly through the openings on the head or at the apex of the metasoma. The sting serves as the chief means of offense and defense (Dolichoderinae and Formicinae lack a sting). All ants can bite, and some bite rather severely. Some ants give off or eject from the anus a foul-smelling substance that serves as defense. Many ant secretions act as alarm substances, some stimulate group activity, and many (laid down by a foraging individual) serve as an odor trail that other individuals can follow. Some of these secretions appear to play a role in caste determination.

Subfamily Ecitoninae: The Ecitoninae are the army ants. They are mostly tropical, but one genus (*Eciton*) occurs in the southern and southwestern sections of the United States. These ants are nomadic and often travel in distinct files or "armies." They are highly predaceous. The queens in this group are wingless.

Subfamily Cerapachyinae: This subfamily is represented in North America by three very rare species in Arizona and Texas. The colonies are usually small, a few dozen individuals or less. These ants are predaceous.

Subfamilies Ponerinae, Amblyoponinae, Ectatomminae, and Procereratiinae: In these poneromorph subfamilies, the pedicel is only one-segmented, but there is a distinct constriction between the next two segments posterior to the pedicel (Figure 28–11A). The only common genus in the East is *Ponera*. The workers are 2–4 mm long, and the queens are only a little larger. These ants form small colonies and nest in rotten logs or stumps or in the soil beneath various objects. They feed on other insects. In the tropics, ponerines are important predators.

Subfamily Pseudomyrmecinae: These ants are very slender and nest in hollow twigs, galls, and other cavities in plants. They are largely arboreal in habit. The five North American species are restricted to the southern United States.

Subfamily Myrmicinae: This is the largest subfamily of ants (300 North American species), and its members can usually be recognized by the fact that the pedicel of the metasoma has two segments (Figure 28–11B). The members of this group are widely distributed and vary considerably in habits. The ants in the genera *Pogonomyrmex* and *Pheidole* are often called "harvester ants." They feed on seeds and store seeds in their nests. The fungus ants of the genus *Trachymyrmex* feed on fungi that they cultivate in their nests. The leaf-cutting ants (*Atta*) cut pieces of leaves, carry them to their nests, and feed on a fungus grown on these leaves. *Atta texana* (Buckley) is common in some parts of the South and Southwest, and sometimes does considerable damage by leaf-cutting.

The imported fire ants, *Solenopsis invicta* Buren and *S. richteri* Forel, are important pests in the Southeast. They were introduced into Alabama from South America in 1918 and have since spread over much of the Southeast from the Carolinas to Texas. The red imported fire ant, *S. invicta*, is the more common form. The black imported fire ant, *S. richteri*, has a rather limited distribution in a few of the southeastern states. These ants are aggressive insects with a painful sting and, when disturbed, are quick to attack both people and animals. The workers are 3–6 mm long and reddish brown. A mature nest may contain up to 100,000 or more individuals. The nests are hard-crusted mounds that may sometimes be as large as a meter high and a meter across and may be constructed on agricultural land, homesites, school yards, and recreational areas, where they are not only an eyesore but a hazard to people and animals. On farms the mounds may cause damage to agricultural machinery, and many workers are reluctant to work in areas where the ants occur, because of their painful stings. A related native species, *S. molesta* Say, the thief ant, is a common house-infesting species in the South and West. Ants of the genus *Solenopsis* may be distinguished from other myrmicine ants by the fact that the antennae are 10-segmented with a 2-segmented club.

Subfamily Dolichoderinae: In this subfamily and the following one, the pedicel of the metasoma consists of a single segment, and there is no constriction between the next two segments (as in Figure 28–83). This is a small group (19 North American species), and most of its members occur in the southern part of the United States. Most are rather small, the workers being less than 5 mm long. These ants have anal glands that secrete a foul-smelling fluid, which can sometimes be forcibly ejected from the anus for a distance of several centimeters. One species, the Argentine ant, *Linepithema humile* (Mayr), was a common household pest in the southern states before the imported fire ants appeared.

Subfamily Formicinae: This is the second-largest subfamily of ants (200 North American species), and it is widespread in distribution. Habits vary considerably in this group. The genus *Camponotus* includes the carpenter ants, some of which are the largest ants in North America; *C. pennsylvanicus* (DeGeer) is a large black ant that excavates a series of anastomosing galleries in wood for its nests. Unlike termites, the carpenter ants do not feed on the wood.

The ants in the genus *Polyergus* are slave makers and are entirely dependent on slaves. When a *Polyergus* queen starts a new colony, she raids a nest of another species, usually a *Formica*, and kills the queen in that colony. The *Formica* workers then usually adopt the *Polyergus* queen. To maintain the colony, the *Polyergus* ants make raids on *Formica* colonies, killing the workers and carrying off the pupae.

The worker caste of *Polyergus* is given to fighting, whereas the slaves take over the activities of nest building, brood rearing, foraging, and the like. The *Polyergus* ants are often called Amazons. *Polyergus lucidus* Mayr, a brilliant red species, is fairly common in the eastern United States. The genus *Lasius* contains a number of small field ants that make small mound nests and feed largely on honeydew. Many tend aphids, storing the aphid eggs through the winter and placing the young aphids on their food plant in the spring.

Formica is a very large genus, containing about 70 North American species. Many are mound-building species. The mounds of *F. exsectoides* Forel, a common species in the eastern United States, are sometimes 0.6 to 0.9 m high and 2 or more meters across. The United States varieties of *F. sanguinea* Latreille are slave makers, somewhat similar in habits to the Amazon ants. They periodically raid the nests of other species of *Formica* and carry off worker pupae. Some are eaten, but others are reared and take their place in the *sanguinea* colony. The honey ants of the genus *Myrmecocystus*, which occur in the southwestern United States, are of interest in that some individuals (termed "repletes") serve as reservoirs for honeydew collected by other workers.

Collecting and Preserving Hymenoptera

Most of the general collecting methods described in Chapter 35 apply to the insects in this order. Species of Hymenoptera are almost everywhere; to secure a large variety of species, examine all available habitats and use all available methods of collecting. Many of the larger and more showy Hymenoptera are common on flowers. The parasitic species can be reared from parasitized hosts, or they can be taken by sweeping. Passive trapping techniques, such as Malaise traps, flight-intercept traps, and pan traps are extremely effective in capturing a wide diversity of species that would otherwise go unnoticed. A number of species search for hosts or prey underground and are best collected by using Berlese or Winkler funnels.

Because many of the Hymenoptera sting, exercise care in removing them from the net. One way is to get the insect into a fold in the net and then put this fold into the killing jar until the insect is stunned. Another effective method is to get the insect confined in the end of the net (almost all winged aculeates fly upward toward the light), grasp the end of the net from the outside just below the insect, then reach inside with the killing jar and evert the end of the net into the jar, put the top on over the net, and slide the net out between the jar and lid. Some larger ichneumonids can "sting" by jabbing with their short, sharp ovipositor. Any large Hymenoptera should be handled with care. Aside from the pain normally associated with a sting, some people have severe allergic reactions to the venom that can be life-threatening. Many stinging Hymenoptera feeding on flowers can be collected directly into a killing jar without the use of a net. Most Hymenoptera can be easily killed using a jar charged with ethyl acetate. In addition, because they are generally sturdier than Diptera, for example, Hymenoptera can be killed and stored in alcohol and then later dried and mounted. Often, sweeping vegetation and dumping the contents into alcohol is the most time-efficient method for capturing microhymenoptera (see Chapter 35).

Mount the smaller Hymenoptera on a point, or if they are extremely minute, preserve them in liquid or mounted on a microscope slide. It is usually necessary to mount the more minute forms on microscope slides for detailed study. Some of the best characters for identifying bees are in the mouthparts; so extend the mouthparts if possible. Orient all specimens, whether pinned or mounted on points, so the leg and thoracic characters and venation can be easily seen.

References

Aguiar, A. P., and N. F. Johnson. 2003. Stephanidae of America north of Mexico (Hymenoptera). Proc. Entomol. Soc. Wash. 105:467-483.

Ananthakrishnan, T. N. 1984. The Biology of Gall Insects. London: Edward Arnold, 362 pp.

Andrews, F. G. 1978. Taxonomy and host specificity of Nearctic Alloxystinae with a catalog of the world species (Hymenoptera: Cynipidae). Occasional Papers on Entomology, California Department of Food and Agriculture, Sacramento, CA, No. 25, 128 pp.

Austin, A. D., and M. Dowton (Eds). 2000. Hymenoptera. Evolution, Biodiversity and Biological Control. Collingwood, Victoria, Australia: CSIRO Publishing, 468 pp.

Bohart, R. M., and A. S. Menke. 1976. Sphecid Wasps of the World: A Generic Revision. Berkeley: University of California Press, 695 pp.

Bolton, B. 1994. Identification Guide to the Ant Genera of the World. Cambridge, MA: Harvard University Press, 222 pp.

Bolton, B. 1995. A New General Catalogue of the Ants of the World. Cambridge, MA: Harvard University Press, 504 pp.

Bolton, B. 2003. Synopsis and classification of Formicidae. Mem. Amer. Entomol. Inst. 71:1-370.

Brothers, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. Univ. Kan. Sci. Bull. 50(11):483–648.

Carpenter, J. M. 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). Syst. Entomol. 7:11–38.

Carpenter, J. M. 1986. Cladistics of the Chrysidoidea (Hymenoptera). J. N.Y. Entomol. Soc. 94:303–330.

Carpenter, J. M. 1987. Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae). Syst. Entomol. 12:413–431.

Dessart, P., and P. Cancemi. 1987. Tableau dichotomique des genres de Ceraphronoidea (Hymenoptera) avec commentaires et nouvelles espèces. Frustula Entomologica 7–8:307–372.

Evans, H. E. 1978. The Bethylidae of America north of Mexico. Mem. Amer. Entomol. Inst. No. 27, 332 pp.

Evans, H. E. 1987. Order Hymenoptera. In F. Stehr (Ed.), Immature Insects, pp. 597–710. Dubuque, IA: Kendall/Hunt, 754 pp.

Felt, E. P. 1940. Plant galls and gall makers. Ithaca, N.Y.: Comstock. 364 pp.

Fitton, M. G., and I. D. Gauld. 1976. The family-group names of the Ichneumonidae (excluding Ichneumoniae). Syst. Entomol. 1:247-258.

Fitton, M. G., and I. D. Gauld. 1978. Further notes on family-group names of Ichneumonidae (Hymenoptera). Syst. Entomol. 3:245-258.

Frisch, K. von. 1967. The Dance Language and Orientation of Bees. Cambridge, MA: Belknap Press of Harvard University Press, 566 pp.

Frisch, K. von. 1971. Bees, Their Vision, Chemical Senses, and Language, rev. ed. Ithaca, NY: Cornell University Press, 157 pp.

Gauld, I., and B. Bolton. 1988. The Hymenoptera. London: British Museum (Natural History), 332 pp.

Gess, S. K. 1996. The Pollen Wasps: Ecology and Natural History of the Masarinae. Cambridge, MA: Harvard University Press, 340 pp.

Gibson, G. A. P. 1985. Some pro- and mesothoracic characters important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures. Can. Entomol. 117:1395–1443.

Gibson, G. A. P. 1986. Evidence for monophyly and relationships of Chalcidoidea, Mymaridae, and Mymarommatidae (Hymenoptera: Terebrantes). Can. Entomol. 118:205–240.

Gibson, G. A. P., J. T. Huber, and J. B. Woolley (Eds.). 1997. Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera). Ottawa: NRC Research Press, 794 pp.

Goulet, H., and J. T. Huber. 1993. Hymenoptera of the World: An Identification Guide to Families. Research Branch, Agriculture Canada Publication 1894/E, Centre for Land and Biological Resources Research; Ottawa, 668 pp.

Graham, M. W. R. de V. 1969. The Pteromalidae of northwestern Europe (Hymenoptera: Chalcidoidea). Bull. Brit. Mus. (Nat. Hist.) Entomol. Suppl. No. 16. 908 pp.

Hanson, P. E., and I. D. Gauld. 1995. The Hymenoptera of Costa Rica. Oxford, UK: Oxford University Press, 893 pp.

Heraty, J. M. 2002. A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the world. Mem. Amer. Entomol. Inst. No. 68, 367 pp.

Hölldobler, B., and E. O. Wilson. 1990. The Ants. Cambridge, MA: Belknap Press of Harvard University Press, 732 pp.

Johnson, N. F., and L. Musetti. 1999. Revision of the proctotrupoid genus *Pelecinus* Latreille (Hymenoptera: Pelecinidae). J. Nat. Hist. 33:1513–1543.

Kimsey, L. S. 1984. A re-evaluation of the phylogenetic relationships in the Apidae (Hymenoptera). Syst. Entomol. 9:435–441.

Kimsey, L. S., and R. M. Bohart. 1990. The Chrysidid Wasps of the World. Oxford, UK: Oxford University Press, 652 pp.

Krombein, K. V. 1967. Trap-Nesting Wasps and Bees. Washington, DC: Smithsonian Press, 576 pp.

Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks. 1979. Catalog of Hymenoptera in America North of Mexico, 3 vols. Washington, DC: Smithsonian Institution Press, 2735 pp.

Lindauer, M. 1977. Communication Among Social Bees. Cambridge, MA: Harvard University Press, 161 pp.

Lofgren, C. S., W. A. Banks, and B. M. Glancey. 1975. Biology and control of imported fire ants. Annu. Rev. Entomol. 20:1–30.

Marsh, P. M., S. R. Shaw, and R. A. Wharton. 1987. An identification manual for the North American genera of the family Braconidae (Hymenoptera). Mem. Entomol. Soc. Wash. No. 13, 98 pp.

Masner, L. 1976. A revision of the Ismarinae of the New World (Hymenoptera, Proctotrupoidea, Diapriidae). Can. Entomol. 108:1243–1266.

Masner, L. 1980. Key to genera of Scelionidae of the Holarctic region, with descriptions of new genera and species (Hymenoptera: Proctotrupoidea). Mem. Entomol. Soc. Can. 113, 54 pp.

Masner, L., and J. L. García. 2002. The genera of Diapriinae (Hymenoptera: Diapriidae) in the New World. Bull. Amer. Mus. Nat. Hist. 268:1–138.

Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Nat. Hist. 82:151-326.

Michener, C. D. 1974. The Social Behavior of Bees: A Comparative Study. Cambridge, MA: Belknap Press of Harvard University Press, 404 pp.

Michener, C. D. 2000. The Bees of the World. Baltimore: Johns Hopkins University Press, 913 pp.

Michener, C. D., R. J. McGinley, and B. N. Danforth. 1994. The Bee Genera of North and Central America (Hymenoptera: Apoidea). Washington: Smithsonian Institution Press, 209 pp.

Michener, C. D., and M. H. Michener. 1951. American Social Insects. New York: Van Nostrand, 267 pp.

Middlekauff, W. W. 1969. The cephid stem borers of California (Hymenoptera: Cephidae). Bull. Calif. Insect Surv. 11:1–19.

Middlekauff, W. W. 1983. A revision of the sawfly family Orussidae for North and Central America (Hymenoptera: Symphyta, Orussidae). Univ. Calif. Publ. Entomol. 101, 46 pp.

Morse, R. A. 1975. Bees and Beekeeping. Ithaca, NY: Cornell University Press, 296 pp.

Naumann, I. D., and L. Masner. 1985. Parasitic wasps of the proctotrupoid complex: A new family from Australia and a key to world families (Hymenoptera: Proctotrupoidea *sensu lato*). Austral. J. Zool. 33:761–783.

Olmi, M. 1984. A revision of the Dryinidae (Hymenoptera). Mem. Amer. Entomol. Inst. No. 37 (2 vols.), 1913 pp.

Quicke, D. L. J. 1997. Parasitic Wasps. London: Chapman & Hall, 470 pp.

Rasnitsyn, A. P. 1969. Origin and evolution of the lower Hymenoptera [in Russian]. Tr. Paleontol. Inst. 123:1–196.

Rasnitsyn, A. P. 1975. Early evolution of the higher Hymenoptera (Apocrita) [in Russian]. Zool. Zh. 54:848–859.

Rasnitsyn, A. P. 1980. Origin and evolution of the Hymenoptera [in Russian]. Tr. Paleontol. Inst. 174:1–190.

Rasnitsyn, A. P. 1988. An outline of evolution of the hymenopterous insects (Order Vespida). Oriental Insects 22:115–145.

Richards, O. W. 1977. Hymenoptera: Introduction and Key to Families, 2nd ed. Handbooks for the Identification of British Insects, vol. 6(1), 100 pp. [Other papers in this series, by various authors, cover groups within Hymenoptera.] London: Royal Entomological Society of London.

Richards, O. W. 1978. The Social Wasps of the Americas, Excluding the Vespinae. London: British Museum (Natural History), 580 pp.

Ronquist, E 1999. Phylogeny of the Hymenoptera (Insecta): The state of the art. Zool. Scr. 28:3–11.

Ross, H. H. 1936. The ancestry and wing venation of the Hymenoptera. Ann. Entomol. Soc. Amer. 29:99–111.

Ross, H. H. 1937. A generic classification of Nearctic sawflies (Hymenoptera, Symphyta). Ill. Biol. Monogr. No. 15:1–172.

Schneirla, T. C. 1971. Army Ants: A Study in Social Organization. San Francisco: Freeman, 350 pp.

Seeley, T. D. 1985. Honeybee Ecology: A Study of Adaptation in Social Life. Princeton, NJ: Princeton University Press, 201 pp.

Sharkey, M. J. 1993. Family Braconidae. In H. Goulet and J. T. Huber (Eds.), Hymenoptera of the World: A Guide to Families, pp. 362–395. Ottawa: Agriculture Canada.

Smith, D. R. 1969. Key to Genera of Nearctic Argidae (Hymenoptera) with revisions of the genera *Atomacera* Say and *Sterictiphora* Billberg. Trans. Amer. Entomol. Soc. 95:439–457

Smith, D. R. 1969. Nearctic sawflies. Part 1: Blennocampinae: Adults and larvae. USDA Tech. Bull. No. 1397, 179 pp.

Smith, D. R. 1969. Nearctic sawflies. Part 2: Selandriinae: Adults. USDA Tech. Bull. No. 1398, 48 pp.

Smith, D. R. 1971. Nearctic sawflies. Part 3: Heterarthrinae: Adults and larvae. USDA Tech. Bull. No. 1429, 84 pp.

Smith, D. R. 1974. Conifer sawflies, Diprionidae: Key to North American genera, checklist of world species, and new species from Mexico. Proc. Entomol. Soc. Wash. 76:409–418.

Smith, D. R. 1976. The xiphydriid woodwasps of North America. Trans. Entomol. Soc. Amer. 102:101–131.

Smith, D. R. 1979. Nearctic sawflies. Part 4: Allantinae: Adults and larvae. USDA Tech. Bull. No. 1595, 172 pp.

Townes, H. 1948. The serphoid Hymenoptera of the family Roproniidae. Proc. U.S. Natl. Mus. 98:85–89.

Townes, H. 1949. The Nearctic species of the family Stephanidae (Hymenoptera). Proc. U.S. Natl. Mus. 99:361–370.

Townes, H. 1949. The Nearctic species of Evaniidae (Hymenoptera). Proc. U.S. Natl. Mus. 99:525–539.

Townes, H. 1950. The Nearctic species of Gasteruptiidae (Hymenoptera). Proc. U.S. Natl. Mus. 100:85–145.

Townes, H. 1956. The Nearctic species of trigonalid wasps. Proc. U.S. Natl. Mus. 106:295–304.

Townes, H. 1969–1971. The genera of Ichneumonidae. Part 1 (1969), Mem. Amer. Entomol. Inst. No. 11, 300 pp. Part 2 (1969), Mem. Amer. Entomol. Inst. No. 12, 537 pp. Part 3 (1969), Mem. Amer. Entomol. Inst. No. 13, 307 pp. Part 4 (1971), Mem. Amer. Entomol. Inst. No. 17, 372 pp.

Townes, H. 1977. A revision of the Rhopalosomatidae (Hymenoptera). Contrib. Amer. Entomol. Inst. 15(1), 34 pp.

Townes, H. 1977. A revision of the Heloridae (Hymenoptera). Contrib. Amer. Entomol. Inst. 15(2), 12 pp.

Townes, H., and V. K. Gupta. 1962. Ichneumon-flies of America north of Mexico. Part 4: Subfamily Gelinae, tribe Hemigasterini. Mem. Amer. Entomol. Inst. No. 2, 305 pp.

Townes, H., and M. Townes. 1978. Ichneumon-flies of America north of Mexico. Part 7: Subfamily Banchinae, tribes Lissonotini and Banchini. Mem. Amer. Entomol. Inst. No. 26, 614 pp.

Townes, H., and M. Townes. 1981. A revision of the Serphidae (Hymenoptera). Mem. Amer. Entomol. Inst. No. 32, 541 pp. [Includes both Proctotrupidae and Vanhorniidae.]

van Achterberg, C. 1984. Essay on the phylogeny of Braconidae (Hymenoptera: Ichneumonoidea). Entomol. Tidskr. 105:41–58.

Waage, J., and D. Greathead (Eds.). Insect Parasitoids. New York: Academic Press, 389 pp.

Wharton, R. A., P. M. Marsh, and M. J. Sharkey (Eds.). 1997. Manual of the New World genera of the family Braconidae (Hymenoptera). Special Publication International Society of Hymenopterists 1:1–439.

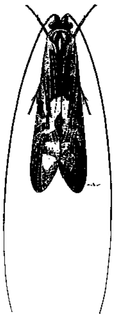
Wilson, E. O. 1971. The Insect Societies. Cambridge, MA: Harvard University Press, 548 pp.

Yu, D. S., and K. Horstmann. 1997. A catalogue of world Ichneumonidae (Hymenoptera). Mem. Amer. Entomol. Inst. 58. 1558 pp.

29

Order Trichoptera[1,2]

Caddisflies



The caddisflies are small to medium-sized insects, somewhat similar to moths in general appearance. The four, membranous wings are rather hairy (and occasionally also bear scales), and at rest they are usually held rooflike over the abdomen. The antennae are long and slender. Most caddisflies are rather dull-colored insects, but a few are conspicuously patterned. The mouthparts are of the chewing type, with the palps well developed but with the mandibles much reduced. The adults feed principally on liquid foods. Caddisflies undergo complete metamorphosis, and the larvae are aquatic.

Caddisfly larvae are caterpillar-like, with a well-developed head and thoracic legs and a pair of hook-like appendages at the end of the abdomen. The abdominal segments sometimes bear filamentous gills (Figure 29–1). Caddisfly larvae live in various types of aquatic habitats. Some live in ponds or lakes, and others live in streams. Some larvae are case makers, others construct nets under water, and a few are free-living.

The cases of the case-making larvae are made of bits of leaves, twigs, sand grains, pebbles, or other materials and are of various shapes (Figure 29–8). Each species builds a very characteristic type of case, and in some species the young larvae build a case different from that made by older larvae. The materials used in making the case are fastened together with silk, or they may be cemented together. Case-making larvae usually eat living or dead plant material. The nets of the net-making species (found in streams) are made of silk spun from modified salivary glands and may be trumpet-shaped, finger-shaped, or cup-shaped, with the open end facing upstream. They are often attached to the side of a rock or other object over which the water flows. The larvae spend their time near these nets (in a retreat of some sort) and feed on the materials caught in the nets. The free-living caddisfly larvae, which construct neither cases nor nets, are generally predaceous.

The larvae fasten their cases to some object in the water when they have completed their growth, seal the opening (or openings) in the case, and pupate in the case. When the pupa is fully developed, it cuts its way out of the case with its mandibles (which are well developed in this stage), swims to the surface, then crawls out of the water onto a stone, stick, or similar object, and the adult emerges.

The wing venation of caddisflies (Figures 29–2A, 29–3) is rather generalized, and there are few crossveins. The subcosta is usually two-branched, the radius five-branched, the media four-branched in the front wing and three-branched in the hind wing, and the cubitus three-branched. The anal veins in the front wing usually form two Y-shaped veins near the base of the wing. Most species have a characteristic wing spot in the fork of R_{4+5}. Cu_2 in the hind wing usually fuses basally with 1A for a short distance. In naming the cubital and anal veins in this order, we follow the interpretation of Ross (1944) and others rather than that of Comstock (1940). The veins we call Cu_{1a} and Cu_{1b} are called Cu_1 and Cu_2, respectively, by Comstock, who considers the remaining veins to be anal veins. In some groups (for example, Figure 29–2A), the basal part of Cu_1 in the front wing appears like a crossvein.

The majority of the caddisflies are rather weak fliers. The wings are vestigial in winter in the females

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[1] Trichoptera: *tricho*, hair; *ptera*, wings.

[2] This chapter benefited from the editing and substantive additions by John C. Morse, Tatyana S. Vshivkov, and David Ruiter.

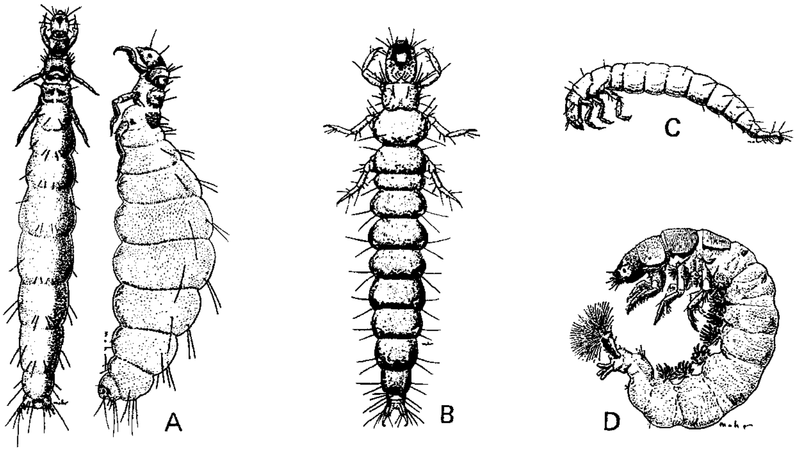


Figure 29–1 Caddisfly larvae. A, *Hydroptila waubesiana* Betten (Hydroptilidae), dorsal view at left, lateral view at right; B, *Rhyacophila fenestra* Ross (Rhyacophilidae); C, *Polycentropus interruptus* (Banks) (Polycentropidae); D, *Hydropsyche simulans* Ross (Hydropsychidae). (Courtesy of Ross and the Illinois Natural History Survey.)

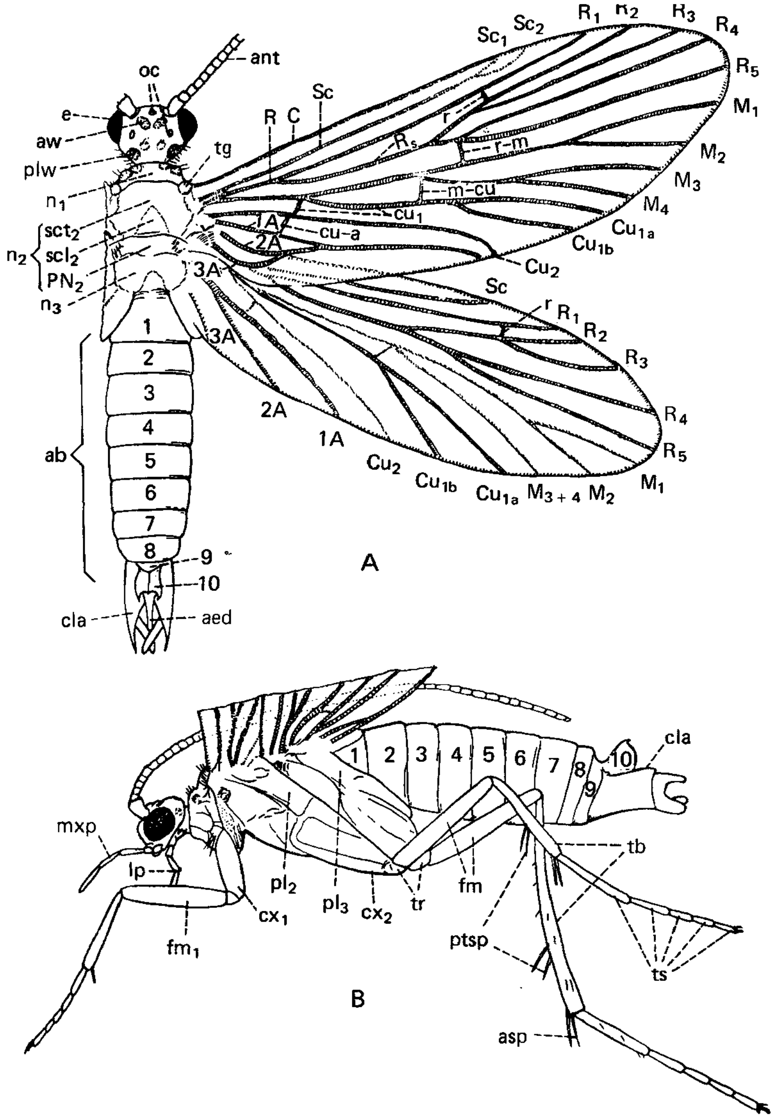


Figure 29–2 Structure of a caddisfly. A, dorsal view; B, lateral view. *ab*, abdomen; *aed*, aedeagus; *ant*, antenna; *asp*, apical spur; *aw*, anterior wart; *cla*, clasper; *cx*, coxa; *e*, compound eye; *fm*, femur; *lp*, labial palp; *mxp*, maxillary palp; n_1, pronotum; n_2, mesonotum; n_3, metanotum; *oc*, ocelli; pl_2, mesopleuron; pl_3, metapleuron; *plw*, posterolateral wart; PN_2, postnotum of mesothorax; *ptsp*, preapical tibial spur; scl_2, mesoscutellum; sct_2, mesoscutum; *tb*, tibia; *tg*, tegula; *tr*, trochanter; *ts*, tarsus; *1–10*, abdominal segments. (Redrawn from Ross [1944].)

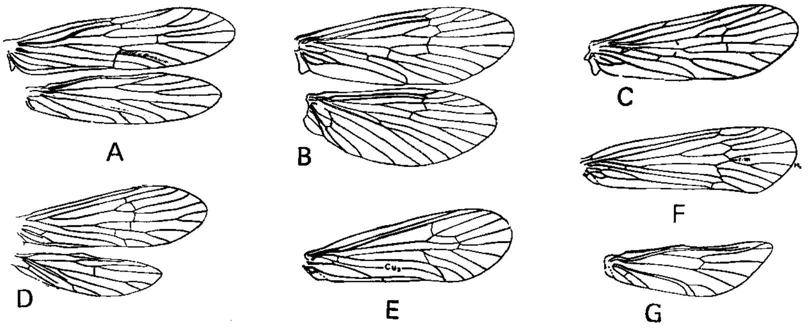


Figure 29–3 Wings of Trichoptera. A, *Dibusa angata* (Ross) (Hydroptilidae); B, *Homoplectra doringa* (Milne) (Hydropsychidae); C, front wing of *Dolophilodes distinctus* (Walker) (Philopotamidae); D, *Psychomyia nomada* (Ross) (Psychomyiidae); E, front wing of *Agarodes crassicornis* (Walker) (Sericostomatidae); F, front wing of *Phanocelia canadensis* (Banks) (Limnephilidae); G, hind wing of *Helicopsyche borealis* (Hagen) (Helicopsychidae). (Courtesy of Ross and the Illinois Natural History Survey.)

of one species, *Dolophilodes distinctus* (Walker). The eggs are laid in masses or strings of several hundred, either in the water or on objects near the water. The adult in many species enters the water and attaches its eggs to stones or other objects. The eggs usually hatch in a few days, and in most species the larva requires nearly a year to develop. The adults usually live about a month. Adult caddisflies are frequently attracted to lights.

The chief biological importance of this group lies in the fact that the larvae are an important part of the food of many fish and other aquatic animals. Their communities are often used as an indication of the amount of pollution in streams.

Classification of the Trichoptera

The arrangement of families followed here is that of the Trichoptera World Checklist (Morse 2001) which recognizes 26 families in North America. This arrangement, with other arrangements or spellings in parentheses, is outlined as follows. Families that are rare or unlikely to be encountered by the general collector are indicated by an asterisk (*).

Superfamily Hydropsychoidea
  Dipseudopsidae (Polycentropodidae in part)*
  Ecnomidae*
  Hydropsychidae—net-spinning caddisflies
  Polycentropodidae (Polycentropidae; Psychomyiidae in part)—trumpet-net and tube-making caddisflies
  Psychomyiidae—tube-making and trumpet-net caddisflies
  Xiphocentronidae*

Superfamily Philopotamoidea
  Philopotamidae—finger-net caddisflies or silken-tube spinners

Superfamily Hydroptiloidea
  Glossosomatidae (Rhyacophilidae in part)—saddle-case makers
  Hydroptilidae—microcaddisflies

Superfamily Rhyacophiloidea
  Hydrobiosidae (Rhyacophilidae in part)*
  Rhyacophilidae—primitive caddisflies

Superfamily Limnephiloidea
  Apataniidae (Limnephilidae in part)
  Goeridae (Limnephilidae in part)*
  Limnephilidae—northern caddisflies
  Rossianidae (Limnephilidae in part)
  Uenoidae (Limnephilidae in part)*
  Brachycentridae
  Lepidostomatidae*

Superfamily Phryganeoidea
  Phryganeidae—large caddisflies

Superfamily Leptoceroidea
  Odontoceridae
  Calamoceratidae
  Leptoceridae—long-horned caddisflies
  Molannidae

Superfamily Sericostomatoidea
  Beraeidae*
  Helicopsychidae—snail-case caddisflies
  Sericostomatidae*

Characters Used in Identifying Trichoptera

The characters used in separating families of adult caddisflies are principally those of the head and thoracic warts, the ocelli, the maxillary palps, the spurs and spines on the legs, and the wing venation.

The head and thoracic warts, which are of considerable value in separating families, are well-defined wartlike or tubercle-like structures on the dorsum of the thorax. They usually bear many larger bristles, distinct from the fine, short clothing hairs elsewhere on the notum. These bristles are sometimes not confined to warts, but may be distributed in linear or diffuse setal areas (e.g., Figures 29–4C, 29–4H). They vary in size, number, and arrangement, and some of these variations are shown in Figure 29–4. These warts are very difficult to interpret in pinned specimens, because they are often destroyed or distorted by the pin. For this and other reasons, caddisflies should be preserved in alcohol rather than on pins.

The maxillary palps are nearly always five-segmented in females, but they may contain fewer segments in the males of some groups. The size and form of particular segments may differ in different families (Figure 29–5). Some variation in the spination of the legs is shown in Figure 29–6. The most important variations are in the number of tibial spurs, which may vary up to a maximum of four—two apical and two preapical spurs near the middle of the tibia. Wing venation is not a very important character in separating the families of caddisflies.

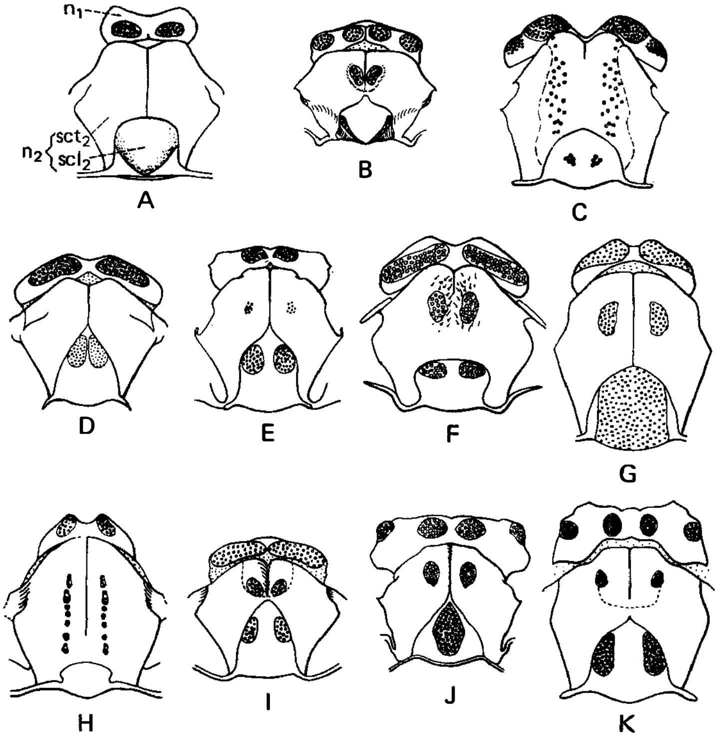


Figure 29–4 Pro- and mesonota of Trichoptera. A, *Hydropsyche simulans* Ross (Hydropsychidae); B, *Psychomyia flavida* Hagen (Psychomyiidae); C, *Ceraclea tarsipunctata* (Vorhies) (Leptoceridae); D, *Beraea gorteba* Ross (Beraeidae); E, *Brachycentrus numerosus* (Say) (Brachycentridae); F, *Helicopsyche borealis* (Hagen) (Helicopsychidae); G, *Psilotreta frontalis* Banks (Odontoceridae); H, *Heteroplectron americanum* (Walker) (Calamoceratidae); I, *Agarodes crassicornis* (Walker) (Sericostomatidae); J, *Goera calcarata* Banks (Goeridae); K, *Theliopsyche* sp. (Lepidostomatidae). n_1, pronotum; n_2, mesonotum; scl_2, mesoscutellum; sct_2, mesoscutum. (Courtesy of Ross and the Illinois Natural History Survey.)

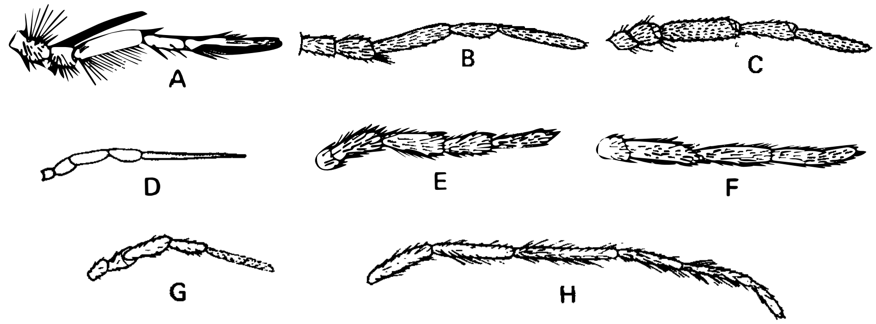


Figure 29–5 Maxillary palps of Trichoptera. A, *Psilotreta* sp., male (Odontoceridae); B, *Dolophilus shawnee* Ross, male (Philopotamidae); C, *Rhyacophila lobifera* Betten, male (Rhyacophilidae); D, *Macrostemum zebratum* (Hagen) (Hydropsychidae); E, *Banksiola selina* Betten, female (Phryganeidae); F, *B. selina*, male; G, *Cyrnellus marginalis* (Banks) (Psychomyiidae); H, *Triaenodea tardus* Milne, male (Leptoceridae). (Courtesy of Ross and the Illinois Natural History Survey.)

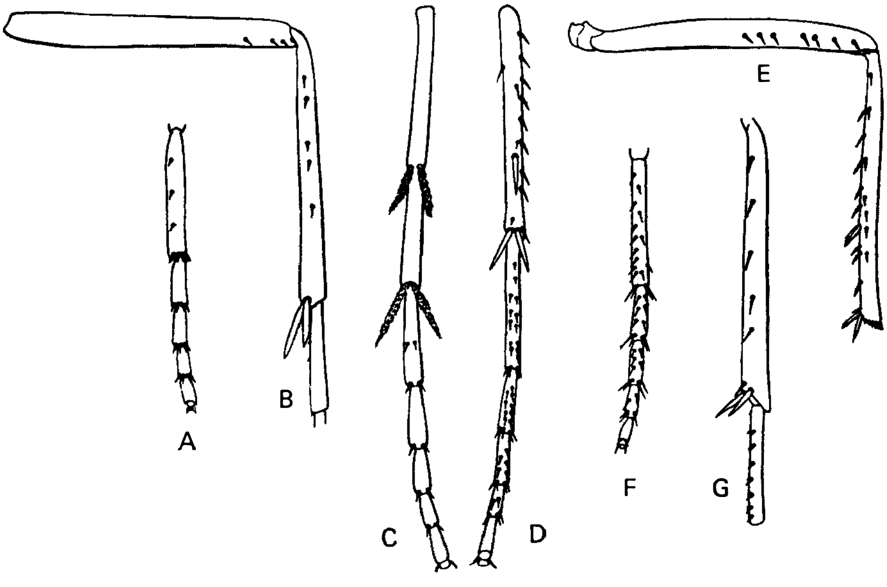


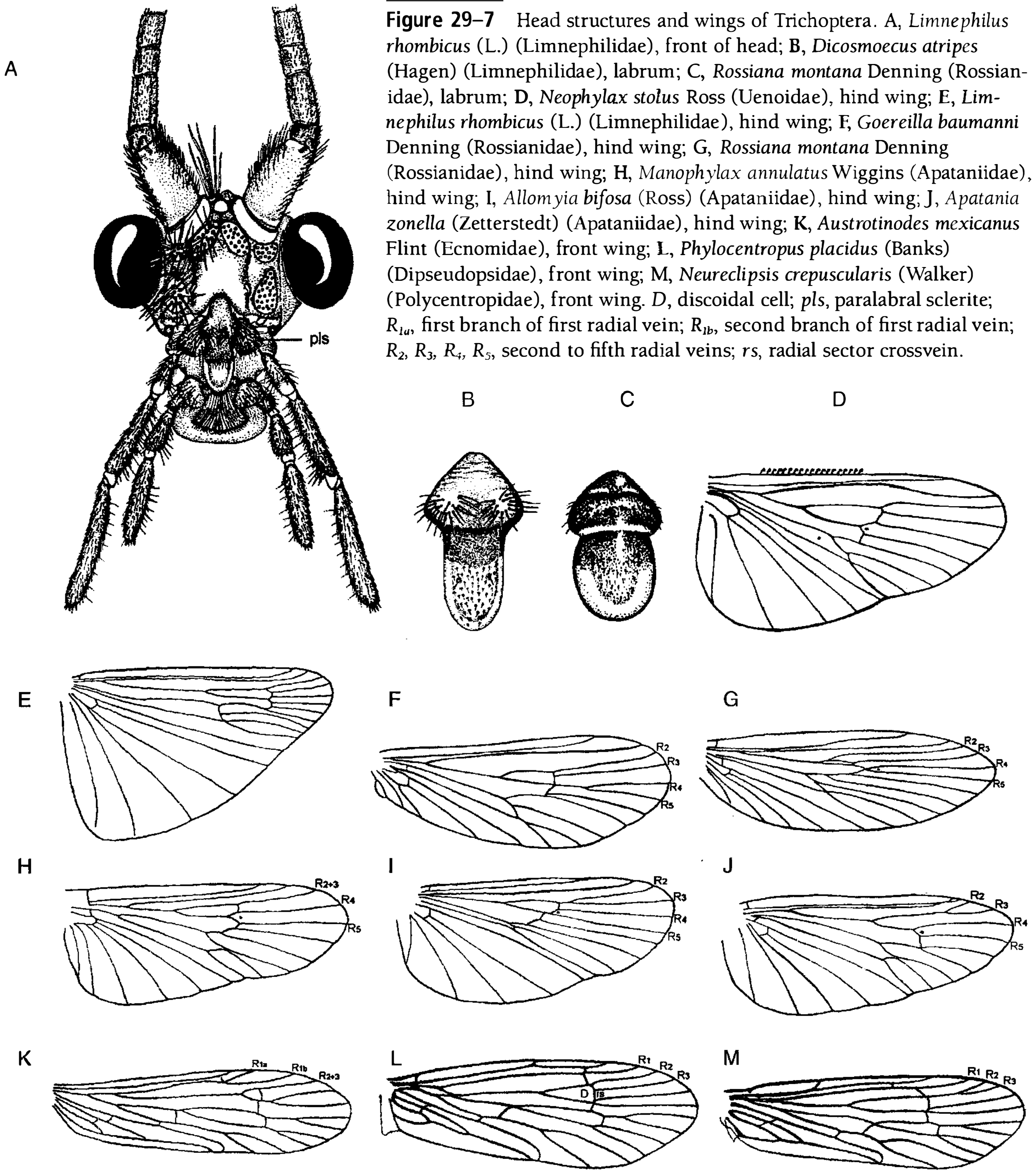
Figure 29–6 Legs of Trichoptera. A, middle tarsus of *Beraea gorteba* Ross (Beraeidae); B, middle leg of *B. gorteba*; C, middle tibia and tarsus of *Theliopsyche corona* Ross (Lepidostomatidae); D, middle tibia and tarsus of *Brachycentrus numerosus* (Say) (Brachycentridae); E, middle leg of *Molanna uniophila* Vorhies (Molannidae); F, middle tarsus of *Agarodes crassicornis* (Walker) (Sericostomatidae); G, middle tibia of *Agarodes crassicornis*. (Courtesy of Ross and the Illinois Natural History Survey.)

Key to the Families of Trichoptera

Families marked with an asterisk (*) in the key are small or unlikely to be encountered by the general collector. Keys to larvae are given by Wiggins (1996a, 1996b).

1.	Mesoscutellum with posterior portion forming a flat triangular area with steep sides, and mesoscutum without warts; some wing hairs clubbed; hind wings narrow and pointed apically, often with a posterior fringe of hairs as long as wing is wide; antennae short (Figure 29–9F); small insects, usually less than 6 mm long	Hydroptilidae	p. 567
1′.	Mesoscutellum evenly convex, without a triangular portion set off by steep sides, or mesoscutum with warts; no wing hairs clubbed; hind wings usually broader and rounded apically; posterior fringe if present of shorter hairs; antennae usually as long as or longer than wings; length 5–40 mm	2	
2(1′).	Ocelli present	3	
2′.	Ocelli absent	12	
3(2).	Maxillary palps 5-segmented, fifth segment 2 or 3 times as long as fourth (Figure 29–5B)	Philopotamidae	p. 566
3′.	Maxillary palps with 3–5 segments, if 5-segmented then fifth segment about the same length as the fourth	4	
4(3′).	Maxillary palps 5-segmented, second segment short, often more or less rounded, about same length as first segment (Figure 29–5C)	5	
4′.	Maxillary palps with 3–5 segments, if 5-segmented then second segment slender, longer than first	8	
5(4).	Second segment of maxillary palps rounded or globose (Figure 29–5C); widely distributed	6	
5′.	Second segment of maxillary palps cylindrical, not globose; U.S. Southwest	Hydrobiosidae*	p. 567
6(5).	Front tibiae with a preapical spur	Rhyacophilidae	p. 567
6′.	Front tibiae without a preapical spur	7	
7(6′).	Pronotal warts widely separated	Glossosomatidae	p. 567
7′.	Pronotal warts close together but not actually in contact (*Palaeagapetus*)	Hydroptilidae*	p. 567
8(4′).	Middle tibiae with 2 preapical spurs	Phryganeidae	p. 569
8′.	Middle tibiae with 1 preapical spur	9	
9(8′).	Costal margin of hind wing with row of stout, hooked setae (Figure 29–7D); paralabral setae and sclerites absent	Uenoidae*	p. 569
9′.	Costal margin of hind wing with fine, inconspicuous setae (Figures 29–7E–J); paralabral setae or setose sclerites (*pls*) present (Figure 29–7A)	10	
10(9′).	Small black or dark gray insects (length of fore wing 3–8 mm), without color pattern; labrum short, its basal part almost equal to or only slightly shorter than distal part (Figure 29–7C); anal area of hind wing weakly developed (Figures 29–7F–J)	11	
10′.	Medium to large insects (length of fore wing 12–35 mm), with various colors and patterns; labrum long, its basal part conspicuously shorter than its distal part (Figure 29–7B); anal area of hind wing usually broader (Figure 29–7E)	Limnephilidae	p. 567

Figure 29–7 Head structures and wings of Trichoptera. A, *Limnephilus rhombicus* (L.) (Limnephilidae), front of head; **B**, *Dicosmoecus atripes* (Hagen) (Limnephilidae), labrum; C, *Rossiana montana* Denning (Rossianidae), labrum; **D**, *Neophylax stolus* Ross (Uenoidae), hind wing; E, *Limnephilus rhombicus* (L.) (Limnephilidae), hind wing; F, *Goereilla baumanni* Denning (Rossianidae), hind wing; G, *Rossiana montana* Denning (Rossianidae), hind wing; H, *Manophylax annulatus* Wiggins (Apataniidae), hind wing; I, *Allomyia bifosa* (Ross) (Apataniidae), hind wing; J, *Apatania zonella* (Zetterstedt) (Apataniidae), hind wing; K, *Austrotinodes mexicanus* Flint (Ecnomidae), front wing; L, *Phylocentropus placidus* (Banks) (Dipseudopsidae), front wing; M, *Neureclipsis crepuscularis* (Walker) (Polycentropidae), front wing. *D*, discoidal cell; *pls*, paralabral sclerite; R_{1a}, first branch of first radial vein; R_{1b}, second branch of first radial vein; R_2, R_3, R_4, R_5, second to fifth radial veins; *rs*, radial sector crossvein.



11(10).	Hind wing fork of R_2 and R_3 sessile, arising at or basal of the level of one or more crossveins (Figures 29–7F,G); hind wing fork of R_4 and R_5 distal, arising well beyond any other wing forks or crossveins (Figures 29–7F,G)	Rossianidae	p. 568
11′.	Hind wing fork of R_2 and R_3 absent (Figure 29–7H) or petiolate (Figures 29–7I,J), arising beyond all crossveins; hind wing fork of R_4 and R_5 more nearly basal, arising at level of other wing forks and crossveins (Figures 29–7H–J)	Apataniidae	p. 568
12(2′).	Maxillary palps with 5 or more segments	13	
12′.	Maxillary palps with fewer than 5 segments	19	
13(12).	Terminal segment of maxillary palps much longer than preceding segment, with numerous cross striae that the other segments do not have (Figure 29–5G)	14	
13′.	Terminal segment of maxillary palps without such cross striae, similar in structure and length to preceding segment, or some segments with long hair brushes (Figure 29–5A)	19	
14(13).	Mesoscutum with a pair of warts	15	
14′.	Mesoscutum without warts (Figure 29–4A)	Hydropsychidae	p. 566
15(14).	Mesoscutum with a pair of small, rounded warts that are sometimes touching at midline (Figure 29–4B); widely distributed	16	
15′.	Mesoscutal warts large, somewhat quadrate, continuous along entire midline of mesoscutum; southern Texas	Xiphocentronidae*	p. 566
16(15).	Front tibiae with a preapical spur, or if this spur absent (*Cernotina*, Polycentropodidae) then basal tarsal segment less than twice as long as longer apical spur	17	
16′.	Front tibiae without a preapical spur and basal tarsal segment at least twice as long as the longer apical spur	Psychomyiidae	p. 566
17(16).	R_1 in front wing branched; R_{2+3} not branched (Figure 29–7K); Texas	Ecnomidae*	p. 566
17′.	R_1 in front wing not branched; R_2 and R_3 usually branched (Figures 29–7L,M)	18	
18(17′).	Fork of R_2 and R_3 in front wing originating at radial sector crossvein (rs) which closes the discoidal cell (D) (Figure 29–7L); eastern U.S. and Canada	Dipseudopsidae*	p. 566
18′.	Fork of R_2 and R_3 in front wing originating well beyond radial sector crossvein (Figure 29–7M); widely distributed	Polycentropodidae	p. 566
19(12′, 13′).	Tarsal segments, except basal one, with spines only around apex (Figure 29–6A); mesoscutum lacking warts and setae	Beraeidae*	p. 569
19′.	Tarsal segments with spines arranged irregularly (Figure 29–6F); mesoscutum with warts or setal areas	20	
20(19′).	Mesoscutal setae arising in area extending over almost the entire length of mesoscutum (Figure 29–4C,H)	21	
20′.	Mesoscutal setae usually confined to a pair of warts (Figure 29–4F,G,I,J,K)	23	
21(20).	Basal segment of antennae at most twice as long as second; dorsum of head usually with posteromesal ridge	Calamoceratidae	p. 569
21′.	Basal segment of antennae at least 3 times as long as second; dorsum of head without posteromesal ridge	22	
22(21′).	Antennae much longer than body; middle tibiae without preapical spurs	Leptoceridae	p. 569
22′.	Antennae little if any longer than body; middle tibiae with 2 preapical spurs	Molannidae	p. 569

23(20′).	Warts on dorsum of head very large, extending from eye to midline and anteriorly to middle of head; antennae never longer than front wing	Helicopsychidae	p. 569
23′.	Warts on dorsum of head smaller, not as in preceding entry, or antennae 1.5 times as long as front wings	24	
24(23′).	Mesoscutellum with single, large wart occupying most of sclerite (Figure 29–4G,J)	25	
24′.	Mesoscutellum with a pair of warts, or if appearing to have only 1 (Lepidostomatidae) then wart occupies only about anterior half of the sclerite	26	
25(24).	Mesoscutellar wart occupying most of sclerite (Figure 29–4G); maxillary palps always 5-segmented	Odontoceridae	p. 569
25′.	Mesoscutellar wart elongate and occupying only mesal portion of sclerite (Figure 29–4J); maxillary palps 5-segmented in female, 3-segmented in male	Goeridae*	p. 567
26(24′).	Pronotum with 1 pair of warts; mesoscutum with deep median fissure (Figure 29–4I)	Sericostomatidae*	p. 567
26′.	Pronotum with 2 pairs of warts; median fissure of mesoscutum not as deep as in preceding entry	27	
27(26′).	Middle tibiae with an irregular row, middle tarsi with a double row of spines; middle tibiae with 1–2 preapical spurs situated at about two thirds tibial length (Figure 29–6D), or preapical spurs lacking	Brachycentridae	p. 569
27′.	Middle tibiae without spines, and middle tarsi with only a scattered few in addition to apical ones (Figure 29–6C); middle tibiae with 2 preapical spurs arising from about midlength of the tibia	Lepidostomatidae*	p. 569

Family **Ecnomidae:** This is a Neotropical group; one species has recently been reported in Texas, *Austrotinodes texensis* Bowles.

Family **Polycentropodidae—Trumpet-Net and Tent-Making Caddisflies:** These caddisflies vary in length from 4 to 11 mm. Most are brownish with mottled wings. The larvae live in a variety of aquatic situations: some in rapid streams, some in rivers, and others in lakes. Some (such as *Polycentropus*) construct trumpet-shaped nets that collapse rather rapidly when removed from the water.

Family **Dipseudopsidae—Tube-Making Caddisflies:** Species of the only North American genus (*Phylocentropus*) construct tubes in the sand at the bottoms of streams and cement the walls of these tubes to make a fairly rigid structure.

Family **Psychomyiidae—Tube-Making Caddisflies:** The members of this group are very similar to the Polycentropodidae. They differ in leg characters, as indicated in the key (couplet 16). The larvae of these caddisflies construct silken tubes.

Family **Xiphocentronidae:** This group is represented in North America by three species in southern Texas and Arizona.

Family **Hydropsychidae—Net-Spinning Caddisflies:** This is a large group (151 North American species), and many species are fairly common in small streams. The adults of both sexes have 5-segmented maxillary palps with the last segment elongate (Figure 29–5D). Ocelli are absent, and the mesoscutum lacks warts (Figure 29–4A). Most species are brownish, with the wings more or less mottled. The larvae live in the parts of streams where the current is strongest. They construct a caselike retreat of sand, pebbles, or debris and, near this retreat, construct a cup-shaped net with the concave side of the net facing upstream. The larva feeds on materials caught in the net, and pupation occurs in the caselike retreat. These larvae are quite active, and if they are disturbed while feeding in the net, they back into their retreat very rapidly.

Family **Philopotamidae—Finger-Net Caddisflies or Silken-Tube Spinners:** These caddisflies vary in length from 6 to 9 mm and last segment of the maxillary palps is elongate (Figure 29–5B). They are usually brownish, with gray wings. The winter-emerging females of *Dolophilodes distinctus* (Walker) have vestigial wings, but females emerging in warmer months have normal wings. The larvae live in rapid streams and construct

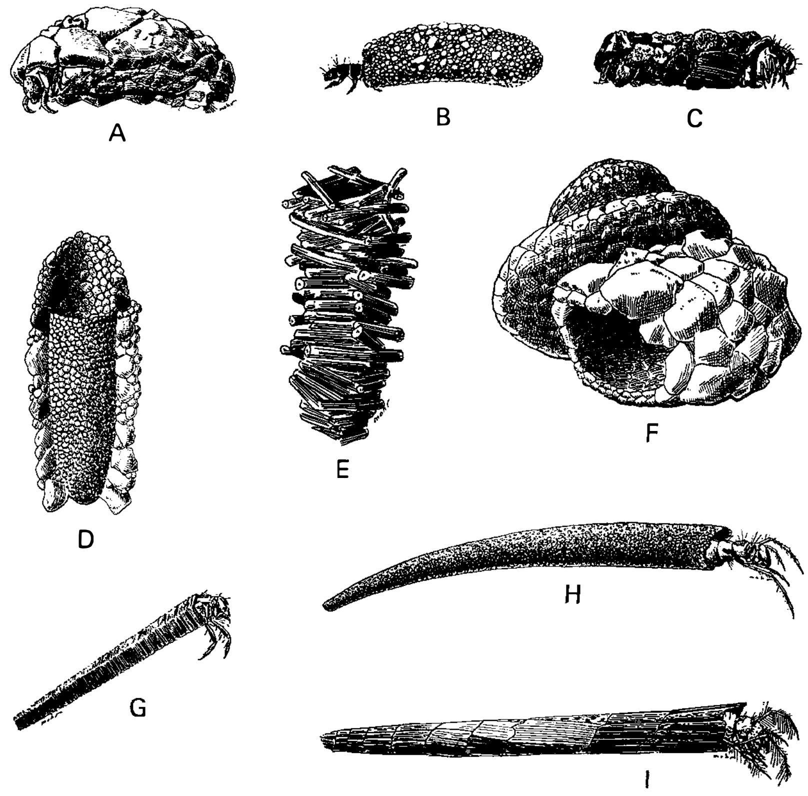


Figure 29–8 Cases of caddisfly larvae. A, *Glossosoma intermedium* (Klapálek) (Glossosomatidae); B, *Ochrotrichia unio* (Ross) (Hydroptilidae); C, *Limnephilus rhombicus* (L.) (Limnephilidae); D, *Molanna uniophila* Vorhies (Molannidae); E, *Oecetis cinerascens* (Hagen) (Leptoceridae); F, *Helicopsyche borealis* (Hagen) (Helicopsychidae); G, *Brachycentrus numerosus* (Say) (Brachycentridae); H, *Nectopsyche albida* (Walker) (Leptoceridae); I, *Triaenodes tardus* Milne (Leptoceridae). (Courtesy of Ross and the Illinois Natural History Survey.)

finger-shaped or tubular nets that are attached to stones. Many such nets are frequently attached close together. The larva stays in the net and feeds on the food caught there; pupation occurs in cases made of pebbles and lined with silk.

Family **Glossosomatidae—Saddle-Case Makers**: The adults in this group are usually brownish with the wings more or less mottled, and they vary in length from 3 to 13 mm. The antennae are short, and the maxillary palps are five-segmented in both sexes. The larvae live in rapid streams. The larvae make saddlelike or turtle-shaped cases (Figure 29–8A). These cases are oval, with the dorsal side convex and composed of relatively large pebbles, and the ventral side is flat and composed of smaller pebbles and sand grains. When these larvae pupate, the ventral side of the case is cut away and the upper part is fastened to a stone.

Family **Hydroptilidae—Microcaddisflies**: This is a large group (263 North American species) of small caddisflies that are 1.5 to 6 mm long. They are quite hairy (Figure 29–9F), and most have a salt-and-pepper mottling. The larvae of most species live in small lakes. These insects undergo a sort of hypermetamorphosis: The early instars are active and do not construct cases, but the last instar does make a case. The anal hooks are much larger in the active instars than in the last instar. The case is usually somewhat purse-shaped, with each end open (Figure 29–8B).

Family **Hydrobiosidae**: The only members of this group in North America are three species of *Atopsyche*, which occur in the Southwest. The larvae do not make cases, and are predaceous.

Family **Rhyacophilidae—Primitive Caddisflies**: These insects are very similar to the Glossosomatidae (which were formerly considered a subfamily of the Rhyacophilidae), but they differ in habits. These caddisflies do not make cases and are predaceous. This is a fairly large group, and all but one of its approximately 127 North American species belong to the genus *Rhyacophila*.

Family **Goeridae**: This a small group that is represented in North America by 11 species. In these caddisflies, the maxillary palps are five-segmented in the females and three-segmented in the males. The larvae live in streams and construct cases of small pebbles, usually with two large pebbles glued to each side acting as ballast.

Family **Limnephilidae—Northern Caddisflies**: This large family has 239 species in North America. Most species are northern in distribution. The adults vary in length from 7 to 23 mm, and most species are brownish with the wings mottled or patterned (Figure 29–9A).

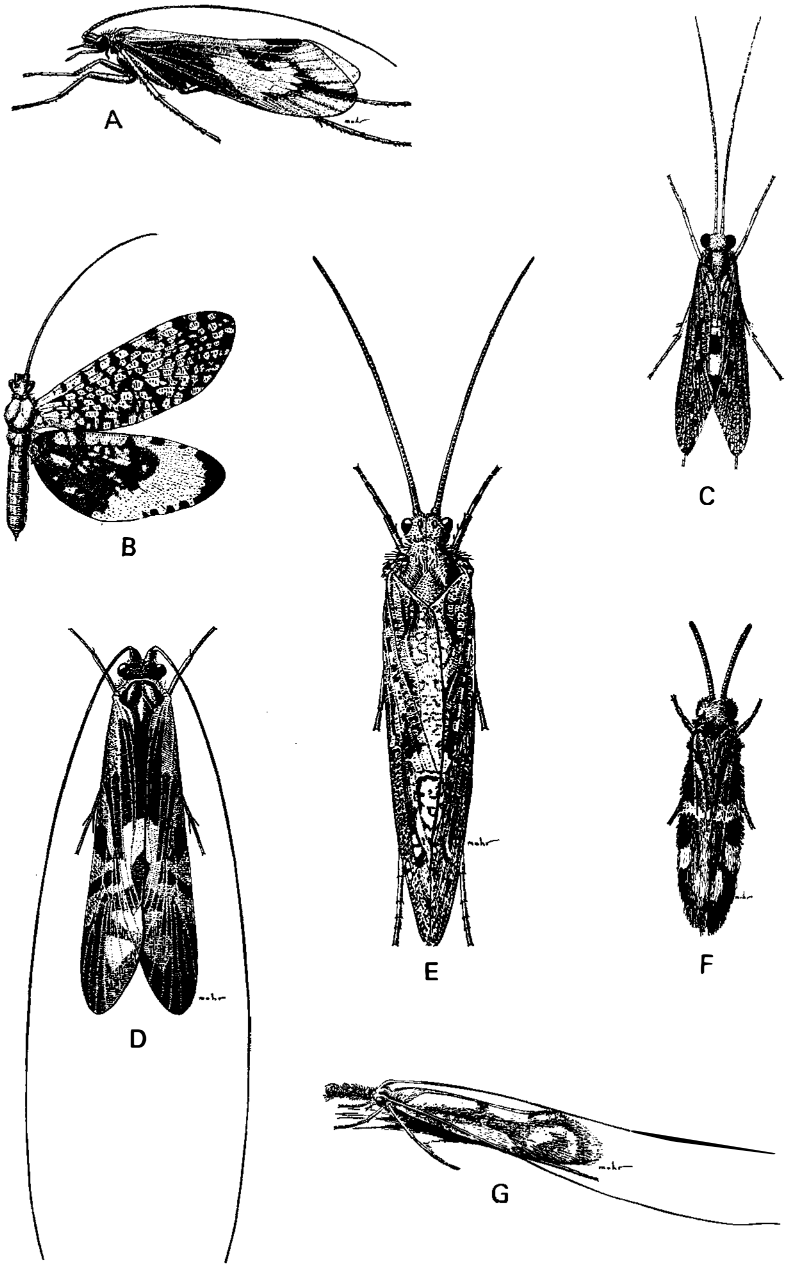


Figure 29–9 Adult caddisflies. A, *Platycentropus radiatus* (Say), male (Limnephilidae); B, *Eubasilissa pardalis* (Walker), female (Phryganeidae); C, *Hydropsyche simulans* Ross, male (Hydropsychidae); D, *Macrostemum zebratum* (Hagen), male (Hydropsychidae); E, *Phryganea cinerea* Walker, male (Phryganeidae); F, *Hydroptila hamata* Morton, male (Hydroptilidae); G, *Triaenodes tardus* Milne, male (Leptoceridae). (Courtesy of Ross and the Illinois Natural History Survey.)

The maxillary palps are three-segmented in the males and five-segmented in the females. The larvae live principally in ponds and slow-moving streams. The cases are made of a variety of materials, and in some species the cases made by the young larvae are quite different from those made by older larvae. The larval stages of one species in this family, *Philocasea demita* Ross, which occur in Oregon, live in moist leaf litter.

Family **Apataniidae:** This family was recently segregated from the family Limnephilidae and includes 24 western species; 7 eastern species; and 3 transcontinental, northern-boreal species. Larvae of *Apatania* are scrapers that browse on algae and other organic material attached on the surface of stones. They graze while protected in sand cases that are tapered and curved posteriorly.

Family **Rossianidae:** This is another family that was recently segregated from the family Limnephilidae. It includes two western species, each in its own genus. Larvae eat fine bits of organic debris in springs and may scrape algae and shred leaves of mosses. Their mineral cases are tapered and curved.

Family **Uenoidae:** This small group has 51 North American species. The larval cases are made of sand grains or small pebbles and are long, slender, tapered, and curved or resemble the cases of Goeridae.

Family **Brachycentridae:** Of the 37 North American species in this family, 33 belong to two genera, *Brachycentrus* and *Micrasema*. The young larvae of *Brachycentrus* live near the shores of small streams, where they feed principally on algae. Older larvae move to midstream and attach their cases (Figure 29–8G) to stones, facing upstream, and feed on both algae and small aquatic insects. The adults are 6–11 mm long and dark brown to black, with the wings often tawny and checkered. The maxillary palps are three-segmented in the males and five-segmented in the females.

Family **Lepidostomatidae:** This group contains two American genera, *Lepidostoma* and *Theliopsyche*, with 68 species (62 of them in *Lepidostoma*). The females have five-segmented maxillary palps, and the maxillary palps of the males are three-segmented or have a curiously modified one-segmented structure. The larvae live principally in streams or springs. Their cases are mostly square in cross section and composed of leaf and bark fragments. The cases of some species are cylindrical and made of sand grains.

Family **Phryganeidae—Large Caddisflies:** The adults of this group are fairly large caddisflies (14–25 mm long), and the wings are usually mottled with gray and brown (Figure 29–9B,E). The maxillary palps are four-segmented in the males (Figure 29–5F) and five-segmented in the females (Figure 29–5E). The larvae live principally in marshes and lakes; only a few are found in streams. The larval cases are slender, cylindrical, open at both ends, and usually made of narrow strips of plant materials glued together longitudinally, usually in rings or a spiral.

Family **Odontoceridae:** The adults in this group are about 13 mm long, the body is blackish, and the wings are grayish brown with light dots. The larvae live in the riffles of swift streams, where they construct cylindrical, often curved, cases of sand. When ready to pupate, large numbers attach their cases to stones, with the cases glued together and parallel.

Family **Calamoceratidae:** The adults of this group are orange-brown or brownish black, with the maxillary palps five- or six-segmented. The larvae live in both still and rapidly flowing water. The cases of most species are flat and composed of large pieces of leaves or bark. Larvae of species of *Heteroplectron* tunnel through the length of a stick or piece of wood, which then serves as a case. This group is small (five North American species), in which two species are eastern and three occur in the West.

Family **Leptoceridae—Long-Horned Caddisflies:** These caddisflies are slender, often pale-colored, 5–17 mm long, and they have long, slender antennae that are often nearly twice as long as the body (Figure 29–9G). This large family includes 112 North American species. The larvae live in a variety of habitats, and there is considerable variation in the types of cases they make. Some species make long, slender, tapering cases (Figure 29–8H,I); some construct cases of twigs (Figure 29–8E); and some construct cornucopia-shaped cases of sand grains or pieces of freshwater sponge.

Family **Molannidae:** This group is small (seven North American species), and the known larvae live on the sandy bottoms of streams and lakes. The larval cases are shield-shaped and consist of a central cylindrical tube with lateral expansions (Figure 29–8D). The adults, which are 10–16 mm long, are usually brownish gray with the wings somewhat mottled, and the maxillary palps are five-segmented in both sexes. The adults at rest sit with the wings curled about the body, which is held at an angle to the surface on which the insect rests.

Family **Beraeidae:** This family contains only three North American species, in the genus *Beraea*, which occur in the Northeast and in Georgia. The adults are brownish and about 5 mm long. The larval cases are curved, smooth, and made of sand grains.

Family **Helicopsychidae—Snail-Case Caddisflies:** This family contains the single genus *Helicopsyche*, with seven North American species. Adults can usually be recognized by the short mesoscutellum with its narrow, transverse warts (Figure 29–4F) and the hamuli on the hind wings (Figure 29–3G). The adults are 5–7 mm long and somewhat straw-colored, with the wings mottled with brownish. The larvae construct cases of sand that are shaped like a snail shell (Figure 29–8F). During development the larvae live on sandy bottoms, and when ready to pupate they attach their cases in clusters on stones. The cases are about 6 mm wide.

Family **Sericostomatidae:** This is a small group (16 North American species), the larvae of which live in both lakes and streams. *Agarodes* and *Fattigia* are eastern genera, and *Gumaga* occurs in the West. The larval cases are usually tapered, curved, short, smooth, and composed of sand grains, sometimes also with wood fragments.

Collecting and Preserving Trichoptera

Caddisfly adults are usually found near water. The habitat preferences of species differ, so to get a large number of species visit a variety of habitats. The adults can be collected by sweeping in the vegetation along the margins of and near ponds and streams, by checking the underside of bridges, and by collecting at lights. The best way of collecting the adults is at lights. Blue lights seem more attractive than other colors.

Caddisfly larvae can be collected by the various methods of aquatic collecting discussed in Chapter 35. Many can be found attached to stones in the water; others will be found among aquatic vegetation; and still others can be collected with a dip net used to scoop up bottom debris or aquatic vegetation.

Preserve both adult and larval caddisflies in 80% alcohol. Adults may be pinned, but pinning frequently damages the thoracic warts that are used in separating families, and most dried specimens are more difficult to identify to species than specimens preserved in alcohol. When using lights (for example, automobile headlights), one can easily collect large numbers by placing a pan containing about 6 mm of alcohol (or water containing a detergent) directly below the light. The insects eventually fly into the alcohol and be caught. Specimens attracted to lights may also be taken directly into a cyanide jar and then transferred to alcohol, or they may be picked off the light by dipping the index finger in alcohol and scooping up the insect rapidly but gently on the wet finger. An aspirator is a useful device for collecting the smaller species.

References

Betten, C. 1934. The caddis flies or Trichoptera of New York State. N.Y. State Mus. Bull. 292:1–570.

Comstock, J. H. 1940. An introducion to entomology. Ninth edition. Ithaca, N.Y.: Comstock Publishing Company, Inc. 1064 pp.

Denning, D. G. 1956. Trichoptera. In R. L. Usinger (Ed.), Aquatic Insects of California, pp. 237–270. Berkeley: University of California Press.

Flint, O. S., Jr. 1973. Studies of Neotropical caddisflies. Part 16: The genus *Austrotinodes* (Trichoptera: Psychomyiidae). Proc. Biol. Soc. Wash. 86(11):127–142.

Holzenthal, R. W., and R. J. Blahnik. 1997. Trichoptera, caddisflies. http://tolweb.org/tree?group=Trichoptera&contgroup=Endopterygota. Accessed February 4, 2004. In D. R. Maddison (Ed.), 2001, Tree of Life Web Project. http://tolweb.org/tree/#top. Accessed February 4, 2004.

Merritt, R. W., and K. W. Cummins (Eds.). 1996. An Introduction to the Aquatic Insects of North America, 3rd ed. Dubuque, IA: Kendall/Hunt, 862 pp.

Morse, J. C. 1993. A checklist of the Trichoptera of North America, including Greenland and Mexico. Trans. Amer. Entomol. Soc. 119:47–93.

Morse, J. C. 1997. Phylogeny of Trichoptera. Annu. Rev. Entomol. 42:427–450.

Morse, J. C. (Ed.). 2001. Trichoptera World Checklist. http://entweb.clemson.edu/database/tricopt/index.htm (8 Jan 2001). Accessed February 4, 2004.

Morse, J. C., and R. W. Holzenthal. 1996. Trichoptera genera. In R. W. Merritt and K. W. Cummins (Eds.), An Introduction to the Aquatic Insects of North America, 3rd ed., pp. 350–386. Dubuque, IA: Kendall/Hunt, 862 pp.

Nimmo, A. P. 1971. The adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and eastern British Columbia and their post-glacial origins. Quaest. Entomol. 7(1):3–234.

Pennak, R. W. 1978. Fresh-Water Invertebrates of the United States, 2nd ed. New York: Wiley Interscience, 803 pp.

Ross, H. H. 1944. The caddis flies or Trichoptera of Illinois. Ill. Nat. Hist. Surv. Bull. 23(1):1–236.

Ross, H. H. 1956. Evolution and Classification of the Mountain Caddisflies. Urbana: University of Illinois Press, 213 pp.

Ross, H. H. 1959. Trichoptera. W. T. Edmondson (Ed.), Fresh-Water Biology, pp. 1024–1049. New York: Wiley.

Ross, H. H. 1967. The evolution and past dispersal of the Trichoptera. Annu. Rev. Entomol. 12:169–206.

Ruiter, D. E. 2000. Generic key to the adult ocellate Limnephiloidea of the Western Hemisphere (Insecta: Trichoptera). Misc. Contrib. Ohio Biol. Surv. No. 5, 22 pp.

Schmid, F. 1970. Le genre *Rhyacophila* et la famille des Rhyacophilidae (Trichoptera). Mem. Soc. Entomol. Can. No. 66, 230 pp.

Schmid, F. 1980. Les insectes et arachnides du Canada. Partie 7, genera des Trichoptères du Canada et des états adjacents. Direction de la Recheuche, Agriculture Canada, Ottawa. 1692, 296 pp.

Schmid, F. 1998. Genera of the Trichoptera of Canada and Adjoining or Adjacent United States. The Insects and Arachnids of Canada, Part 7. Ottawa: NRC Research Press, 319 pp.

Smith, S. D. 1968. The Arctopsychinae of Idaho (Trichoptera: Hydropsychidae). Pan-Pac. Entomol. 44:102–112.

Wiggins, G. B. 1987. Order Trichoptera. In F. W. Stehr (Ed.), Immature Insects, pp. 253–287. Dubuque, IA: Kendall/Hunt, 754 pp.

Wiggins, G. B. 1996a. Larvae of North American Caddisfly Genera (Trichoptera), 2nd ed. Toronto: University of Toronto Press, 401 pp.

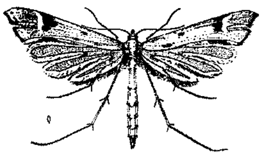
Wiggins, G. B. 1996b. Trichoptera. In R. W. Merritt and K. W. Cummins (Eds.), An Introduction to the Aquatic Insects of North America, pp. 309–349. Dubuque, IA: Kendall/Hunt.

Wiggins, G. B. 1998. The caddisfly family Phryganeidae (Trichoptera). Toronto: University of Toronto Press, 306 pp.

30

Order Lepidoptera[1,2]

Butterflies and Moths



The butterflies and moths are common insects and well known to everyone. They are most readily recognized by the scales on the wings (Figure 30–1), which come off like dust on one's fingers when the insects are handled. Most of the body and legs are also covered with scales. This order is a large one, with more than 11,500 species occurring in the United States and Canada; its members are found almost everywhere, often in large numbers.

The Lepidoptera have considerable economic importance. The larvae of most species are phytophagous, and many are serious pests of cultivated plants. A few feed on fabrics, and a few feed on stored grain or meal. However, the adults of many species are beautiful and much sought by collectors, and many serve as models for art and design. Natural silk is produced by a member of this order.

The mouthparts of a butterfly or moth are usually fitted for sucking. A few species have vestigial mouthparts and do not feed in the adult stage, and the mouthparts in one family (the Micropterigidae) are of the chewing type. The labrum is small and is usually in the form of a transverse band across the lower part of the face, at the base of the proboscis. The mandibles are nearly always lacking. The proboscis, when present, is formed by the appressed, longitudinally grooved galeae of the maxillae and is usually long and coiled. The maxillary palps are generally small or lacking, but the labial palps are nearly always well developed and usually extend forward in front of the face (Figure 30–2B).

The compound eyes of a butterfly or moth are relatively large and consist of a large number of facets. Most moths have two ocelli, one on each side close to the margin of the compound eye. Some species have sensory organs called *chaetosemata* near the ocelli.

Several families have auditory organs called *tympana,* which are believed to function in the detection of the high-frequency echolocating sounds of bats. The Pyraloidea and all the Geometroidea except the Sematuridae have these organs on the anterior sternite of the abdomen, whereas in the Noctuoidea these organs are located ventrolaterally on the metathorax.

The members of this order undergo complete metamorphosis, and their larvae, usually called *cater-*

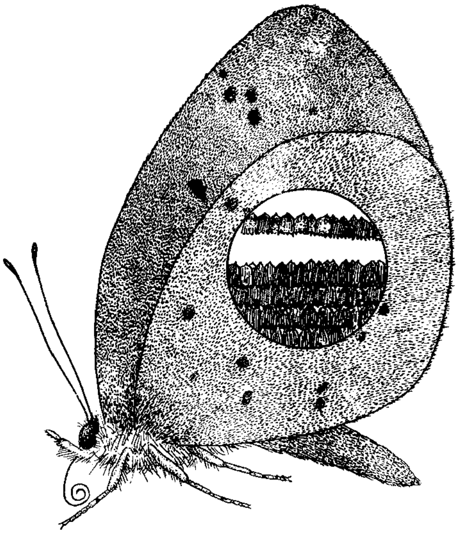


Figure 30–1 A butterfly with a section of the wing enlarged to show the scales.

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[1] Lepidoptera: *lepido*, scale; *ptera*, wings.

[2] This chapter was edited by Ronald W. Hodges, with contributions from Jerry Powell and Steven Passoa.

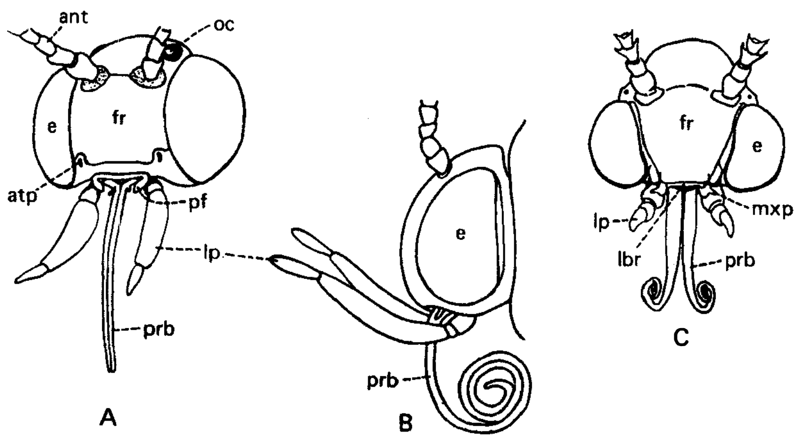

Figure 30–2 Head structure in Lepidoptera. A, *Synanthedon* (Sesiidae), anterior view; B, same, lateral view; C, *Hyphantria* (Arctiidae). *ant*, antenna; *atp*, anterior tentorial pit; *e*, compound eye; *fr*, frons; *lbr*, labrum; *lp*, labial palp; *mxp*, maxillary palp; *oc*, ocellus; *pf*, pilifer; *prb*, proboscis. (Redrawn from Snodgrass.)

pillars, are a familiar sight. Many lepidopteran larvae have a grotesque or ferocious appearance that makes some people afraid of them, but the vast majority are quite harmless when handled. Only a few give off an offensive odor, and only a very few temperate species have stinging body hairs. The ferocious appearance probably plays a role in defense by deterring potential predators.

The larvae of Lepidoptera are usually eruciform (Figure 30–3), with a well-developed head and a cylindrical body of 13 segments (3 thoracic and 10 abdominal). The head usually has six stemmata on each side, just above the mandibles, and a pair of very short antennae. Each thoracic segment bears a pair of legs, and abdominal segments 3–6 and 10 usually bear a pair of prolegs. The prolegs differ somewhat from the thoracic legs. They are more fleshy and lack segmentation, and they usually bear at their apex a number of tiny hooks called *crochets.* Some larvae, such as the measuringworms and loopers, have fewer than five pairs of prolegs, and some lycaenids and leaf-mining microlepidoptera have neither legs nor prolegs. The only other eruciform larvae likely to be confused with those of the Lepidoptera are the larvae of sawflies. Sawfly larvae (Figure 28–37) have only one ocellus on each side, the prolegs do not have crochets, and generally have more than five pairs of prolegs. Most sawfly larvae are 25 mm long or less, whereas many lepidopteran larvae are considerably larger.

Most butterfly and moth larvae feed on plants, but different species feed in different ways. The larger larvae generally feed at the edge of the leaf and consume all but the larger veins; the smaller larvae skeletonize the leaf or eat small holes in it. Many larvae are leaf miners,

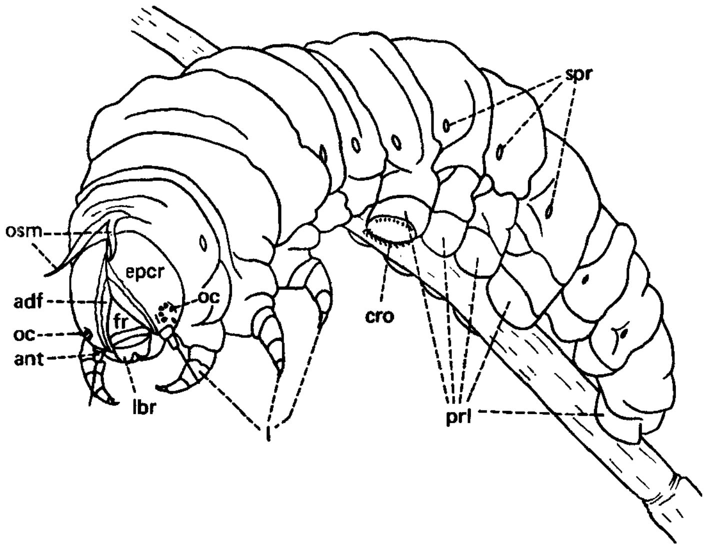

Figure 30–3 Larva of *Papilio* (Papilionidae). *adf*, adfrontal area; *ant*, antenna; *cro*, crochets; *epcr*, epicranium; *fr*, frons; *l*, thoracic legs; *lbr*, labrum; *osm*, osmeterium (scent gland); *prl*, prolegs; *spr*, spriracles; *st*, stemmata.

feeding inside the leaf, and their mines can be linear, trumpet shaped, or blotchlike. A few are gall makers, and a few bore in the fruits, stems, wood, or other parts of the plant. A very few are predaceous on other insects.

The larvae of Lepidoptera have well-developed silk glands, which are modified salivary glands that open on the labium. Many larvae use this silk in making a cocoon, and some use it in making shelters. Leaf rollers and leaf folders roll or fold up a leaf, tie it in place with silk, and feed inside the shelter so formed. Other larvae tie a few leaves together and feed inside this shelter. Some of the gregarious species, such as the tent caterpillars and webworms, make a large shelter involving many leaves and even entire branches.

Pupation occurs in various situations. Many larvae form an elaborate cocoon and transform to the pupa inside it. Others make a very simple cocoon, and still others make no cocoon at all. Many larvae pupate in some sort of protected situation. The pupae (Figure 30–4) are usually obtect, with the appendages firmly attached to the body. Moth pupae are usually brownish and relatively smooth, whereas butterfly pupae are variously colored and are often tuberculate or sculptured. Most butterflies do not make a cocoon, and their pupae are often called *chrysalids* (singular, *chrysalis*). The chrysalids of some butterflies (Nymphalidae, Danainae, Satyrinae, and Libytheinae) are attached to a leaf or twig by the cremaster, a spiny process at the posterior end of the body, and hang head downward (Figure 30–4B). In other cases (Lycaenidae, Pieridae, and Papilionidae), the chrysalis is attached by the cremaster, but it is held in a more or less upright position by a silken girdle about the middle of the body (Figure 30–4A). Some moth larvae (certain Sphingidae, Saturniidae, and Pyralidae) pupate underground. A few moth larvae construct elaborate cocoons, for example, the network cocoon of *Urodus* (Urodidae), which is attached to a branch by a long, silken stalk.

Most Lepidoptera have one generation a year, usually overwintering as a larva or pupa. A few have two or more generations a year, and a few require 2 or 3 years to complete a generation. Many species overwinter in the egg stage; some overwinter as adults.

Classification of the Lepidoptera

Entomologists have made several arrangements of the major groups of Lepidoptera. One of the first was the division of the order into two suborders, Rhopalocera (butterflies) and Heterocera (moths), based principally on antennal characters. Later the order came to be divided into two suborders on the basis of wing venation and the nature of the wing coupling: the Jugatae or Homoneura and the Frenatae or Heteroneura; the Jugatae usually had a jugum (and lacked a frenulum) and a similar venation in the front and hind wings, whereas the Frenatae usually had a frenulum (but no a jugum) and a reduced venation in the hind wings.

Past authorities have recognized two major divisions within the order, the microlepidoptera and the macrolepidoptera (referring to the insects' average size). As used in this book (and by most authorities using these terms), the microlepidoptera include the Monotrysia and the ditrysian superfamilies Tineoidea, Gelechioidea, Yponomeutoidea, and Tortricoidea.

Most recent arrangements have separated the Micropterigidae into a suborder by itself, the Zeugloptera (some authorities consider this an order, related to the Lepidoptera and Trichoptera), with the remaining Lepidoptera divided into two suborders, the Monotrysia and the Ditrysia, based principally on the number of genital openings in the female. This arrangement places the Eriocraniidae, Acanthopteroctetidae, Hepialidae, Nepticu-

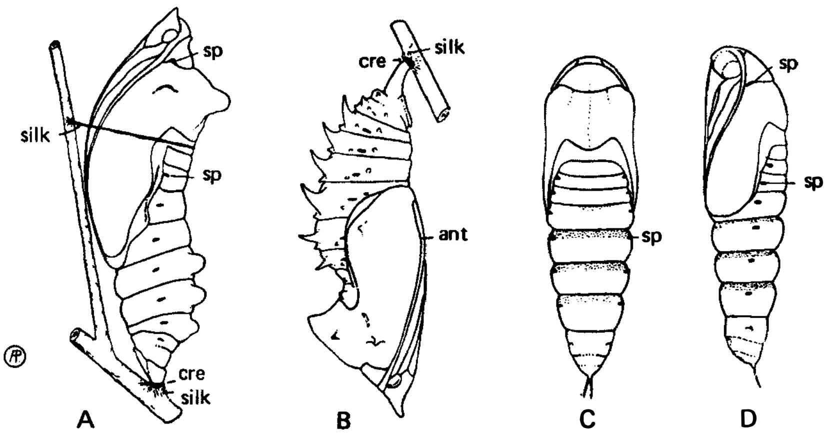

Figure 30–4 Pupae of Lepidoptera. A, *Papilio* (Papilionidae); B, *Nymphalis* (Nymphalidae); C, *Helicoverpa* (Noctuidae), dorsal view; D, same, lateral view. *cre*, cremaster; *sp*, spiracle. (Courtesy of Peterson. Reprinted by permission.)

loidea, and Incurvarioidea in the Monotrysia and the rest in the Ditrysia.

Some authorities (for example, Common 1975) believe the Eriocraniidae, Acanthopteroctetidae, and Hepialidae differ sufficiently from the other groups originally included in the Monotrysia to remove them from that suborder and place them in two separate suborders, the Dacnonypha (for the Eriocraniidae and Acanthopteroctetidae) and the Exoporia (for the Hepialidae and some related exotic families).

Many authors presented a review of the classification of the Lepidoptera in Kristensen (1998) that eliminates suborders and treats superfamilies as the basic units of higher classification. This classification is tentative in many areas but reflects what is currently known about the world fauna. Several rearrangements have been made since the Hodges et al. checklist (1983), the classification used in this book and outlined next (with alternate spellings, names, or arrangements in parentheses). The families marked with an asterisk (*) either are very rare or are unlikely to be taken by a general collector.

Superfamily Micropterigoidea (Micropterygoidea)
  Micropterigidae (Micropterygidae)*

Superfamily Eriocranioidea
  Eriocraniidae*

Superfamily Acanthopteroctetoidea
  Acanthopteroctetidae*

Superfamily Hepialoidea
  Hepialidae

Superfamily Nepticuloidea (Stigmelloidea)
  Nepticulidae (Stigmellidae)*
  Opostegidae*

Superfamily Incurvarioidea
  Heliozelidae*
  Adelidae
  Prodoxidae (Incurvariidae, in part)
  Incurvariidae

Superfamily Tischerioidea
  Tischeriidae*

Superfamily Tineoidea
  Tineidae (Tinaeidae, including Hieroxestidae = Oinophilidae)
  Acrolophidae
  Psychidae (including Talaeporiidae)

Superfamily Gracillarioidea
  Douglasiidae*
  Bucculatricidae (Bucculatrigidae)
  Gracillariidae (Lithocolletidae, Phyllocnistidae)

Superfamily Yponomeutoidea
  Yponomeutidae (Hyponomeutidae, including Attevidae, Prayidae, Scythropiidae, and Argyresthiidae)
  Ypsolophidae (Hypsolophidae, including Ochsenheimeriidae)
  Plutellidae
  Acrolepiidae*
  Glyphipterigidae (Glyphipterygidae)
  Heliodinidae (Schreckensteiniidae)
  Bedellidae*
  Lyonetiidae*

Superfamily Gelechioidea
  Elachistidae (Stenomatidae, Ethmiidae, Azinidae, Depressariidae [Epigraphiidae, Cryptolechiidae, Haemilidae, Thalamarchellidae], Elachistidae [Cycnodiidae, Aphelosetiidae], Agonoxenidae [Blastodacnidae, Parametriotidae])
  Xyloryctidae (Scythrididae)
  Glyphidoceridae
  Oecophoridae ([Dasyceridae], Stathmopodidae, [Tinaegeriidae, Ashinagidae])
  Batrachedridae*
  Deoclonidae*
  Coleophoridae ([Haploptilidae, Eupistidae], Momphidae [Lavernidae], Blastobasidae, Pterolonchidae)
  Autostichidae (Symmocidae)*
  Peleopodidae*
  Amphisbatidae (Oecophoridae, in part)
  Cosmopterigidae (Cosmopterygidae, including Walshiidae)
  Gelechiidae (Anacampsidae, Litidae, Anomologidae, Anarsiidae)

Superfamily Zygaenoidea
  Epipyropidae*
  Megalopygidae (Lagoidae)*
  Limacodidae (Cochliidae, Eucleidae)
  Dalceridae (Acragidae)*
  Lacturidae*
  Zygaenidae

Superfamily Sesiodea
  Sesiidae (Aegeriidae)

Superfamily Cossoidea
  Cossidae (including Zeuzeridae and Hypoptidae)

Superfamily Tortricoidea
  Tortricidae (including Cochylidae [Phaloniidae], Sparganothidae, Olethreutidae, and Eucosmidae)

Superfamily Galacticoidea
  Galacticidae*

Superfamily Choreutoidea
  Choreutidae

Superfamily Urodoidea
  Urodidae*

Superfamily Schreckensteinioidea
  Schreckensteiniidae

Superfamily Epermenioidea
  Epermeniidae*

Superfamily Alucitoidea
  Alucitidae (Orneodidae)

Superfamily Pterophoroidea
  Pterophoridae (including Agdistidae)

Superfamily Copromorphoidea
  Copromorphidae*
  Carposinidae*

Superfamily Hyblaeoidea
  Hyblaeidae (Noctuidae, in part)*

Superfamily Thyridoidea
  Thyrididae (Pyralidae, in part)*

Superfamily Pyraloidea
  Pyralidae (including Galleriidae, Chrysaugidae, Epipaschiidae, and Phycitidae)
  Crambidae (including Schoenobiidae, Nymphulidae, and Pyraustidae)

Superfamily Hesperioidea
  Hesperiidae (including Megathymidae)

Superfamily Papilionoidea
  Papilionidae (including Parnassiidae)
  Pieridae (Asciidae)
  Lycaenidae (Cupidinidae, Ruralidae, including Riodinidae = Nemeobiidae = Erycinidae)
  Nymphalidae (Argyreidae, including Heliconiidae, Ithomiidae, Libytheidae, Morphidae, Brassolidae, Danaidae, and Satyridae)

Superfamily Drepanoidea
  Drepanidae (including Thyatiridae)*

Superfamily Geometroidea
  Sematuridae*
  Uraniidae (including Epiplemidae)*
  Geometridae

Superfamily Mimallonoidea
  Mimallonidae (Lacosomidae, Perophoridae)*

Superfamily Lasiocampoidea
  Lasiocampidae

Superfamily Bombycoidea
  Bombycidae (including Apatelodidae = Zanolidae)*
  Saturniidae (Attacidae, including Ceratocampidae = Citheroniidae)
  Sphingidae (Smerinthidae)

Superfamily Noctuoidea
  Doidae*
  Notodontidae (including Heterocampidae, and Dioptidae)
  Noctuidae (Phalaenidae, including Plusiidae, Agaristidae, and Cuculliidae)
  Pantheidae (Noctuidae, in part)
  Lymantriidae (Liparidae, Orgyidae)
  Nolidae (Noctuidae, in part)
  Arctiidae (including Lithosiidae, Syntomidae = Amatidae, Ctenuchidae, Eucromiidae, Thyretidae, Pericopidae)

Characters Used in Identifying Lepidoptera

The principal characters used in identifying adult Lepidoptera are those of the wings (venation, method of wing union, wing shape, and scaling). Other characters used include the character of the antennae, mouthparts (principally the palps and proboscis), ocelli (whether present or absent), legs, male and female genitalia, and abdomen, and frequently such general features as size and color.

Wing Venation[3]

The wing venation in this order is relatively simple, because there are few crossveins and rarely extra branches of the longitudinal veins, and the venation is reduced in some groups. Entomologists differ regarding the interpretation of certain veins in the lepidopteran wing. Here we follow Comstock's interpretation (Comstock 1940).

Two general types of wing venation occur in this order, homoneurous and heteroneurous. In homoneurous venation, the venation of the front and hind wings is similar; there are as many branches of R in the hind wing as in the front wing. In heteroneurous venation, the venation in the hind wing is reduced, and Rs is always unbranched.

Homoneurous venation occurs in the superfamilies Micropterigoidea, Eriocranioidea, Acanthopteroctetoidea, and Hepialioidea. These groups have a simple or two-branched subcosta, the radius has five branches (occasionally six), the media has three branches, and there are usually three anal veins (Figure 30–5).

The remaining superfamilies have a heteroneurous venation. The radius in the front wing usually has five branches (occasionally fewer), but in the hind wing the radial sector is unbranched and R_1 usually fuses with the subcosta. The basal portion of the media is atrophied in many cases, so that a large cell, commonly called the *discal cell,* is formed in the central part of the wing. The first anal vein is often atrophied or fused with A_2. A somewhat generalized heteroneurous venation is shown in Figure 30–6.

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[3] Some authorities call the mediocubital crossvein of the Comstock (1940) terminology M_4. The three branches of the media, according to Comstock, are M_1, M_2, and M_3. According to these other authorities, Comstock's Cu_1 and Cu_2 are CuA_1 and CuA_2, his 1A is CuP, his 2A is 1A, and his 3A is 2A.

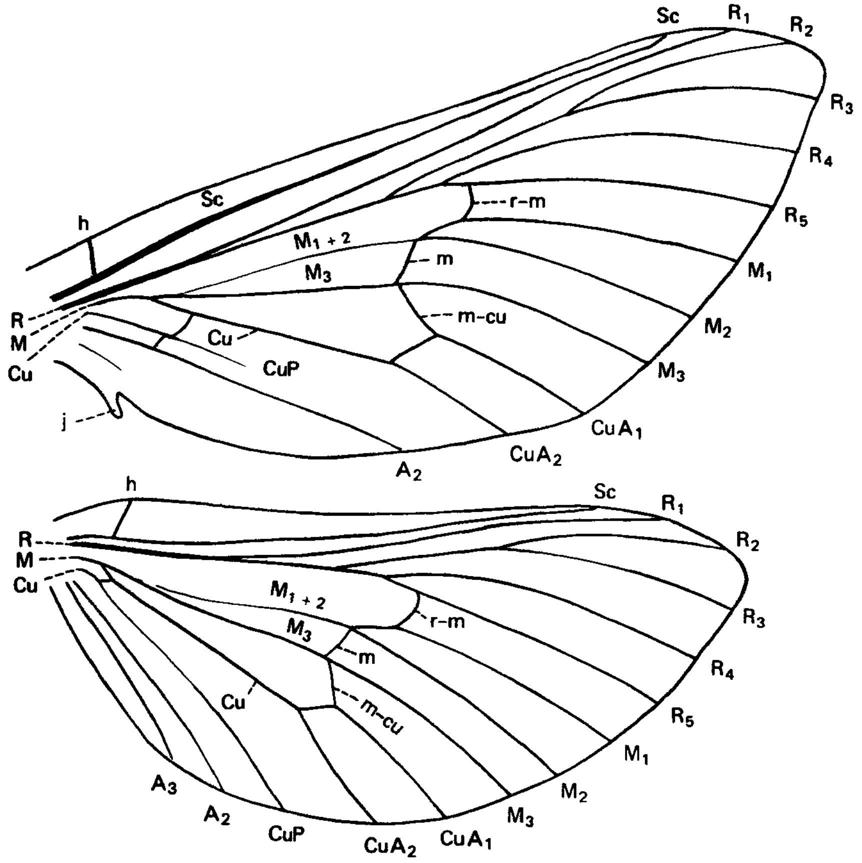

Figure 30–5 Homoneurous venation of *Sthenopis* (Hepialidae). *j*, jugum.

The veins may fuse in various ways in the heteroneurous groups, and this fusing or stalking is used in the key. The subcosta in the front wing is nearly always free of the discal cell and lies between it and the costa. The branches of the radius arise from the anterior side of the discal cell or from its outer anterior corner. Two or more branches of the radius are frequently stalked, that is, fused for a distance beyond the discal cell. Certain radial branches occasionally fuse again beyond their point of separation, thus forming accessory cells (for example, Figure 30–17A, *acc*). The three branches of the media usually arise from the apex of the discal cell in both wings, although M_1 may be stalked with a branch of the radius for a distance beyond the apex of the discal cell (Figure 30–13). The point of origin of M_2 from the apex of the discal cell is an important character used in separating different groups: When it arises from the middle of the apex of the discal cell, as in Figure 30–20, or anterior to the middle, the vein (Cu) forming the posterior side of this cell appears three-branched; when M_2 arises nearer to M_3 than to M_1 (Figures 30–23 through 30–28), then the cubitus appears four-branched.

Variations in the venation of the hind wing of the heteroneurous groups involve principally the nature of the fusion of $Sc+R_1$ and the number of anal veins. In some cases R is separate from Sc at the base of the wing, and R_1 appears as a crossvein between Rs and Sc somewhere along the anterior side of the distal cell (Figure 30–17B). R_1 also fuses with Sc eventually, and judging from the pupal tracheation, the vein reaching the wing margin is Sc (the R_1 trachea is always small); however, this vein at the margin is usually called $Sc+R_1$. In many cases Sc and R are fused basally, or they may be separate at the base and fuse for a short distance along the anterior side of the discal cell (Figures 30–26, 30–27). In the heteroneurous families, most authorities call the 1A of Comstock (1940) CuP; his 2A as A_{1+2}; and his 3A as A_3.

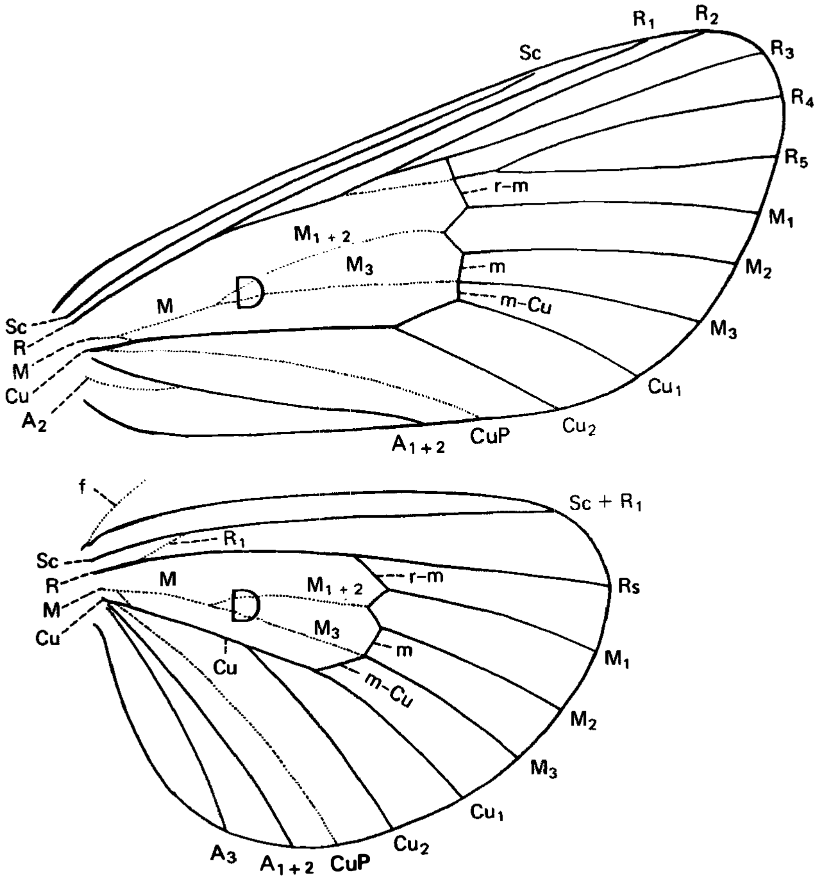

Figure 30–6 Generalized heteroneurous venation. The veins shown by dotted lines are atrophied or lost in some groups. *D*, discal cell; *f*, frenulum.

Other Wing Characters

The wings on each side are made to operate together by four general mechanisms: a fibula, a jugum, a frenulum, and an expanded humeral angle of the hind wing. A fibula is a small, more-or-less triangular lobe at the base of the front wing on the posterior side (Figure 30–34B, *fib*), which overlaps the base of the hind wing. This mechanism occurs in the Micropterigoidea, Eriocranioidea, and Acanthopteroctetoidea. A jugum is a small, fingerlike lobe at the base of the front wing (Figure 30–5, *j*), which overlaps the base of the anterior edge of the hind wing. This structure occurs in the Hepialoidea. A frenulum is a large bristle (acanthus) in males or a group of bristles (most females) arising from the humeral angle of the hind wing and fitting under a group of scales (female) or a sclerotized hook (males), the retinaculum near the costal margin (on the lower surface) of the front wing (Figure 30–6, *f*). A frenulum occurs in most of the other superfamilies (except the butterflies and some moths). Those higher Lepidoptera that lack a frenulum usually have the humeral angle of the hind wing more or less expanded and fitting under the posterior margin of the front wing. A specialized wing coupling of interlocking spines and wing folding occurs in the Sesiidae.

The Nepticuloidea, Incurvarioidea, and Tischeroidea have minute, hairlike spines on the wings (under the scales). These are termed *aculeae*, and such wings may be described as *aculeate* (the aculeae are restricted to the base of the wings in Heliozelidae). The aculeae can be seen when the scales are bleached or removed. They are not movable at the base.

Most Lepidoptera have more or less triangular front wings and somewhat rounded hind wings, but many have more elongate wings. Many smaller microlepidoptera have lanceolate wings; that is, both front and hind wings are elongate and pointed apically, and the hind wings are usually narrower than the front wings (as in Figure 30–33), often with a broad fringe of hairlike scales.

Head Characters

The antennae of butterflies (Figure 30–7A,B) are slender and knobbed at the tip; those of moths (Figure 30–7C–E) are usually filiform, setaceous, or plumose. The basal segment of the antennae in some of the microlepidoptera is enlarged, and when the antenna is bent down and back this segment fits over the eye. Such an enlarged basal antennal segment is called an *eye cap* (Figure 30–29B). Most moths have a pair of ocelli located on the upper surface of the head close to the compound eyes (Figure 30–2A, oc). These ocelli often can be seen only by separating the hairs and scales. The mouthpart characters most often used in keys are the nature of the labial and maxillary palps and the proboscis. Certain exotic families do not conform to these distinctions between moths and butterflies.

Leg Characters

The leg characters of value in identification include the form of the tibial spurs and the tarsal claws, the presence or absence of spines on the legs, and occasionally the structure of the epiphysis. The epiphysis is a movable pad or spurlike structure on the inner surface of the front tibia that is probably used in cleaning the antennae. The front legs are very much reduced in some of the butterflies, particularly the Nymphalidae (Danainae, Satyrinae, and Libytheinae) and males of Riodininae.

Studying Wing Venation in the Lepidoptera

It is often possible to see venational details in a butterfly or moth without any special treatment of the wings, or in some cases by putting a few drops of alcohol or xylene on the wings or by carefully scraping off a few of the wing scales. However, it is often necessary to bleach the wings in order to study all details of wing venation. A method of bleaching and mounting the wings of Lepidoptera is described here.

The materials needed for clearing and mounting lepidopteran wings are as follows:

1. Three watch glasses, one containing 95% alcohol, one containing 10% hydrochloric acid, and one containing equal proportions of aqueous solutions of sodium chloride and sodium hypochlorite (laundry bleach serves fairly well in place of this mixture)
2. A preparation dish of water, preferably distilled water

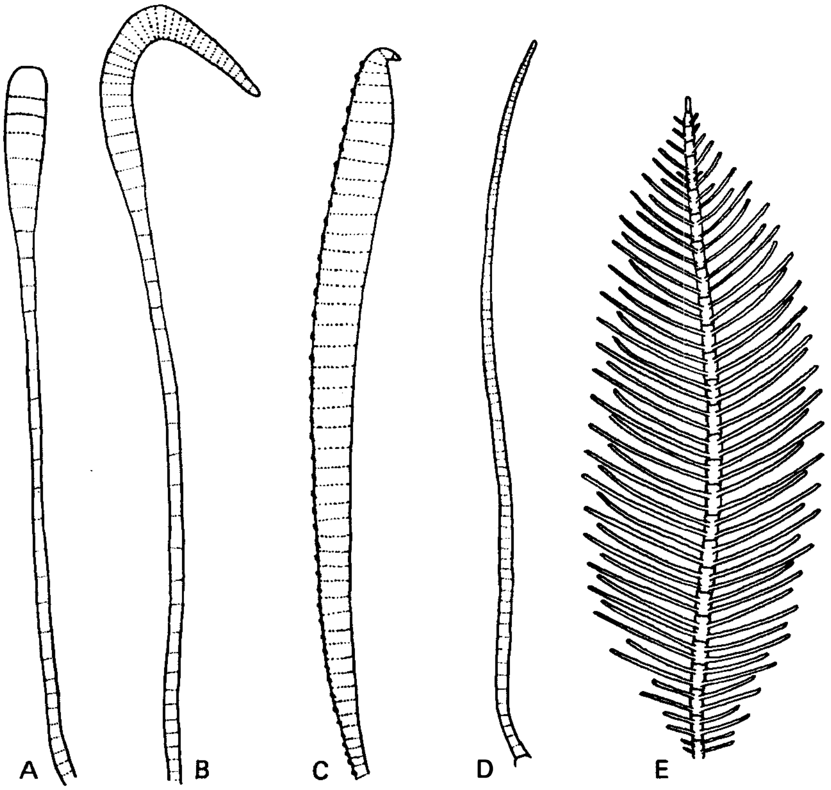

Figure 30–7 Antennae of Lepidoptera. A, *Colias* (Pieridae); B, *Epargyreus* (Hesperiidae); C, *Hemaris* (Sphingidae); D, *Drasteria* (Noctuidae); E, *Callosamia* (Saturniidae).

3. Slides (preferably 50 by 50 mm), masks, and binding tape (or cover slips, and gummed labels with holes cut in the center)
4. Forceps and dissecting needle

The procedure for clearing and mounting the wings is as follows:

1. Remove the wings from one side of the specimen, being careful not to tear them or to break any connections such as the frenulum between the front and hind wings. The frenulum is less likely to be broken if the front and hind wings are removed together.
2. Dip the wings in 95% alcohol for a few seconds to wet them.
3. Dip the wings in 10% hydrochloric acid for a few seconds.
4. Place the wings in the mixture of sodium chloride and sodium hypochlorite (or bleach), and leave them there until the color is removed. This process usually requires only a few minutes. If the wings are slow in clearing, dip them in the acid again and then return them to the bleaching solution.
5. Rinse the wings in water to remove the excess bleach.
6. Place the wings on the slide, centered and properly oriented (preferably with the base of the wings to the left). This procedure is most easily accomplished by floating the wings in water (for example, in a preparation dish) and bringing the slide up from underneath. The wings should be oriented on the slide while they are wet.
7. Allow the slide and wings to dry. If all the bleach has not been removed and some is deposited on the slide, place the slide again in water, carefully remove the wings, clean the slide, and remount the wings.
8. Place the mask on the slide around the wings (put data, labeling, and the like on the mask), put on the cover slide, and bind. Before binding the slide, make sure the wings are dry and both slides are perfectly clean.

Such a slide and the specimen from which the wings have been removed should always be labeled so they can be associated. A wing slide of this sort will keep indefinitely and can be studied under the microscope or projected on a screen for demonstration. In the case of wings 13 mm or less in length, it is better not to use a mask. The mask may be thicker than the wings, and the wings may slip or curl after the slide is bound. The labeling can be put on a small strip of paper that is attached to the outside of the slide with cellophane tape. Small wings can also be mounted under a cover slip, and the cover slip held down with a gummed slide label with a large hole cut from its center.

Key to the Families of Lepidoptera

This key is based to a considerable extent on wing venation, and sometimes it is necessary to wet or mount the wings of a specimen to run it through the key. For the sake of brevity, the two anterior veins in the hind wing are referred to as Sc and Rs, although most of the first vein is usually $Sc+R_1$, and the base of the second vein may be R. Keys to the larvae are given by Forbes (1923–1960), Peterson (1948), and Stehr (1987). The groups marked with an asterisk (*) are relatively rare or are unlikely to be taken by a general collector.

A number of families are based on larval or pupal characters and, therefore, cannot be placed properly in a key based on adult morphology. For that reason, two or more families may key out in the same couplet.

1.	Wings present and well developed	2
1′.	Wings absent or vestigial (females only)	116
2(1).	Front and hind wings similar in venation and usually also in shape; Rs in hind wing 3- or 4-branched (Figures 30–5, 30–34B); front and hind wings usually united by jugum or fibula; no coiled proboscis	3*
2′.	Front and hind wings dissimilar in venation and usually also in shape; Rs in hind wing unbranched; no jugum or fibula, front and hind wings united by frenulum or by expanded humeral angle of hind wing; mouthparts usually in form of a coiled proboscis	6

3(2).	Wingspread 25 mm or more	Hepialidae*	p. 604
3′.	Wingspread 12 mm or less	4*	
4(3′).	Functional mandibles present; middle tibiae without spurs; Sc in front wing forked near its middle (Figure 30–34B)	Micropterigidae*	p. 603
4′.	Mandibles vestigial or absent; middle tibiae with 1 spur; Sc in front wing forked near its tip	5*	
5(4′).	Ocelli present; M_1 in both wings not stalked with R_{4+5}; anal veins in front wing fused distally; widely distributed	Eriocraniidae*	p. 603
5′.	Ocelli absent; M_1 in both wings stalked with R_{4+5}; anal veins in front wing separate; western United States	Acanthopteroctetidae*	p. 603
6(2′).	Antennae threadlike, swollen or knobbed at tip (Figure 30–7A,B); no frenulum; ocelli absent (butterflies and skippers)	7	
6′.	Antennae of various forms, but usually not knobbed at tip (Figure 30–7C–E); if antennae are somewhat clubbed, then frenulum is present; ocelli present or absent (moths)	15	
7(6).	Radius in front wing 5-branched, with all branches simple and arising from discal cell (Figure 30–8); antennae widely separated at base and usually hooked at tip (Figure 30–7B); hind tibiae usually with a middle spur; stout-bodied insects (skippers)	Hesperiidae	p. 619
7′.	Radius in front wing 3- to 5-branched, and if 5-branched, then with some branches stalked beyond discal cell (Figures 30–9 through 30–14); antennae close together at base, never hooked at tip (Figure 30–7A); hind tibiae never with middle spur (butterflies)	8	

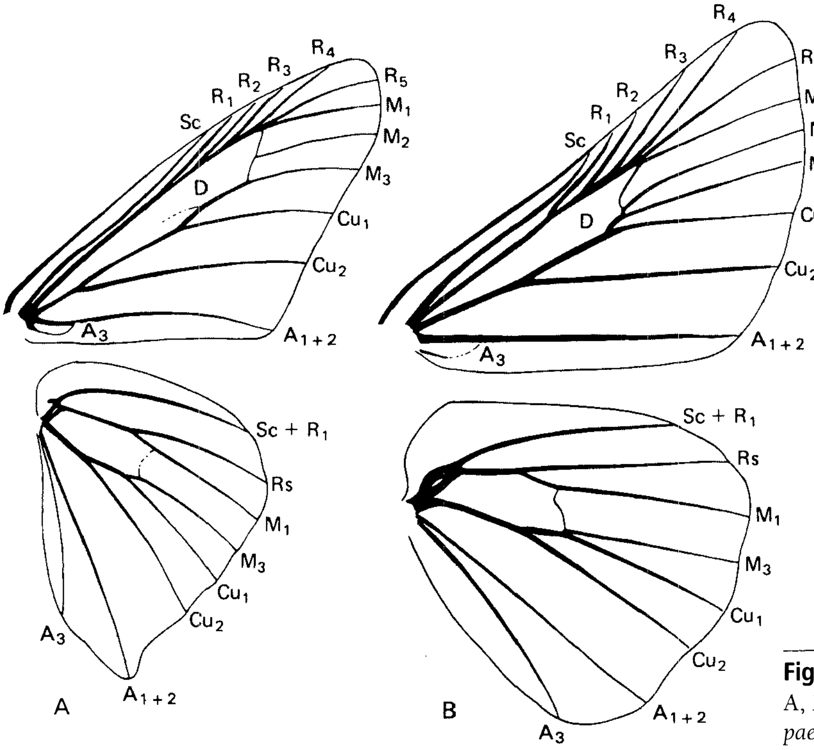

Figure 30–8 Wings of Hesperiidae. A, *Epargyreus* (Pyrginae); B, *Pseudocopaeodes* (Hesperiinae). *D*, discal cell.

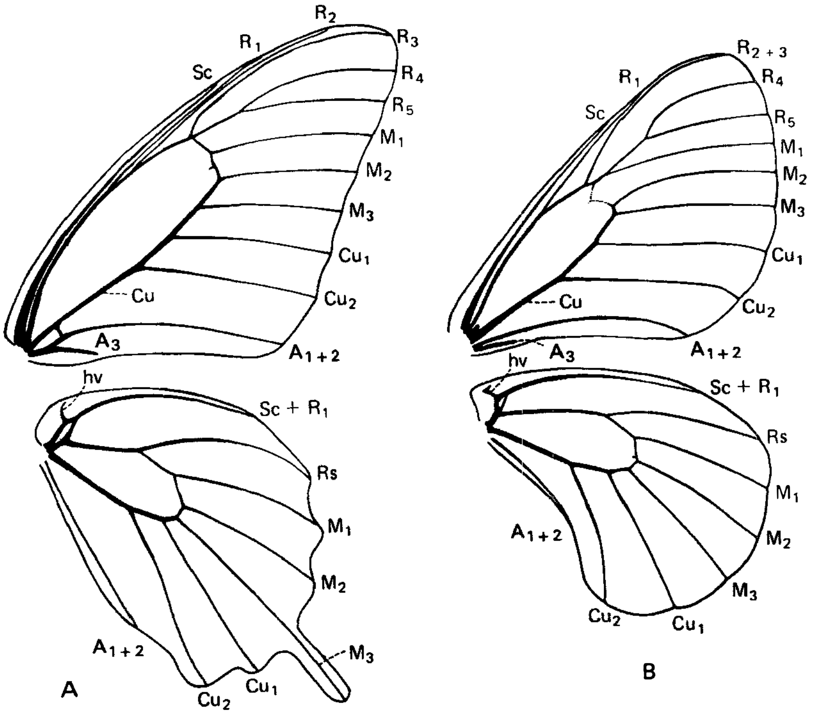

Figure 30–9 Wings of Papilionidae. A, *Papilio* (Papilioninae); B, *Parnassius* (Parnassiinae). *hv*, humeral vein.

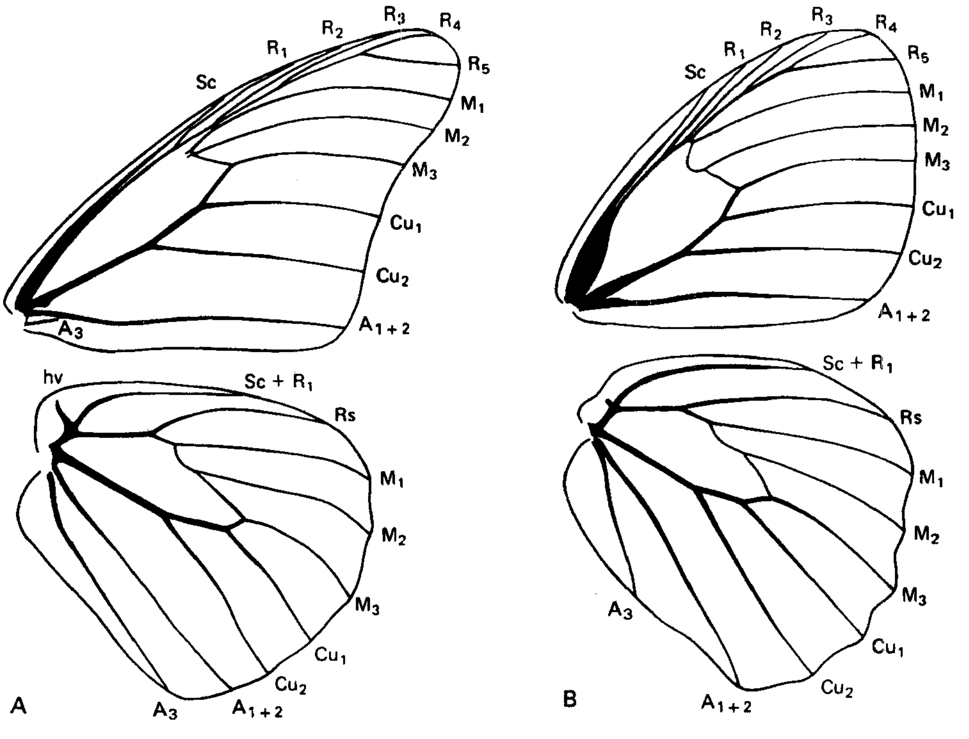

Figure 30–10 Wings of butterflies. A, *Danaus* (Nymphalidae, Danainae); B, *Cercyonis* (Nymphalidae, Satyrinae). *hv*, humeral vein.

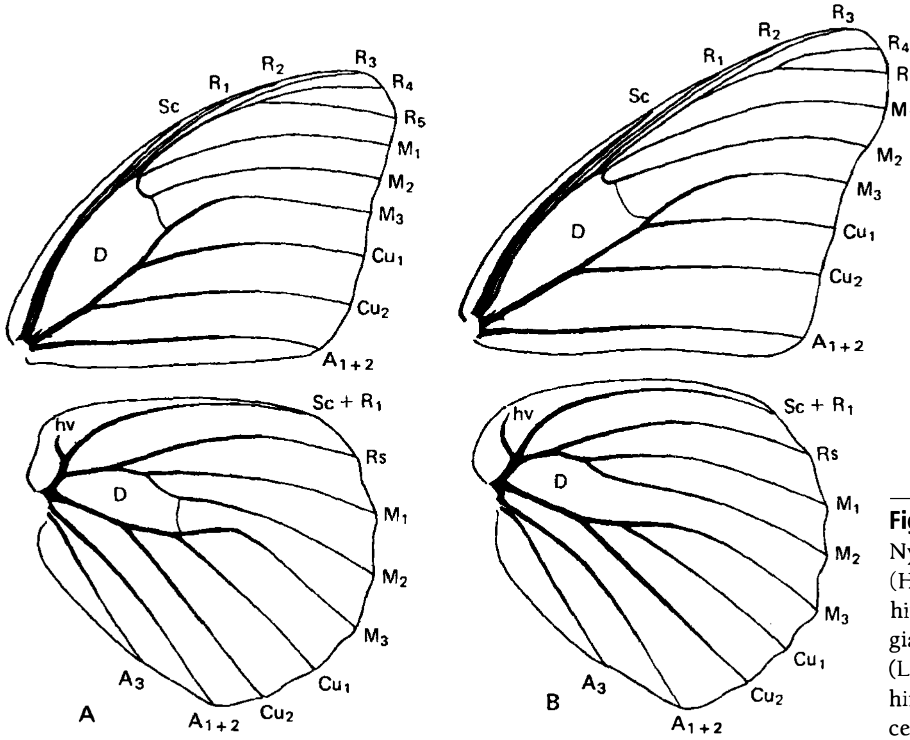

Figure 30–11 Wings of Nymphalidae. A, *Speyeria* (Heliconiinae) (discal cell in hind wing closed by a vestigial vein); B, *Limenitis* (Limenitinae) (discal cell in hind wing open). *D*, discal cell; *hv*, humeral vein.

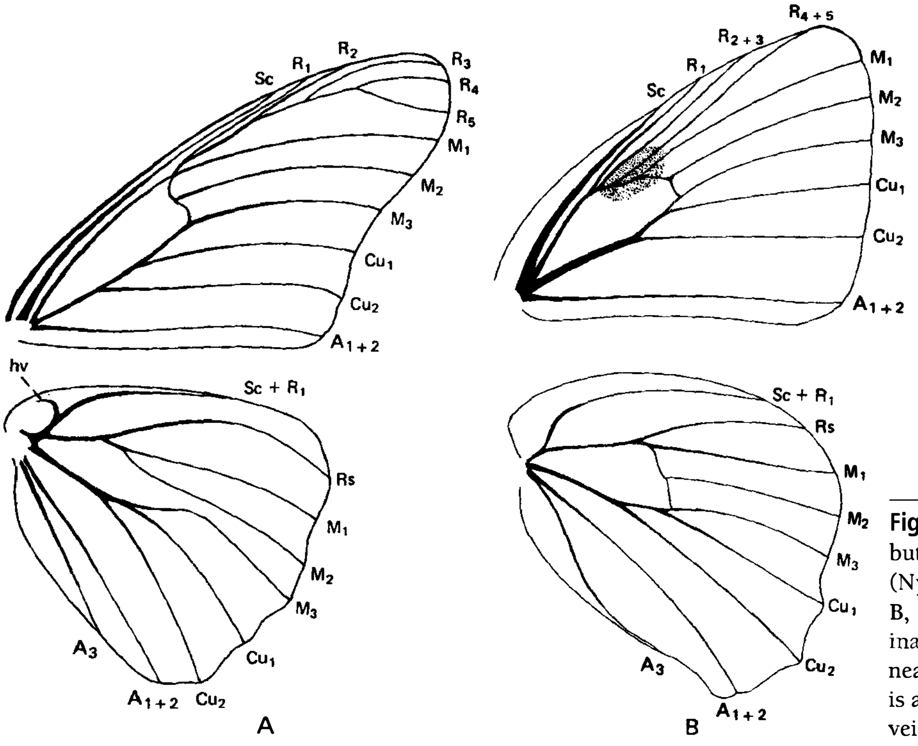

Figure 30–12 Wings of butterflies. A, *Agraulis* (Nymphalidae, Heliconiinae); B, *Thecla* (Lycaenidae, Lycaeninae), male. The dark spot near the end of the discal cell, is a scent gland. *hv*, humeral vein.

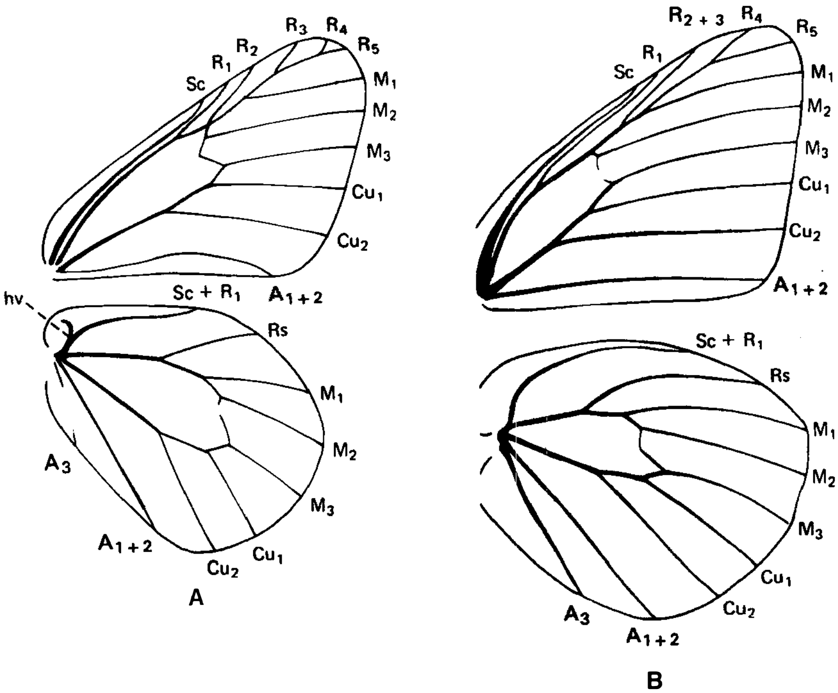

Figure 30–13 Wings of Pieridae. A, an orange-tip (*Euchloe*); B, a sulphur (*Colias*). *hv*, humeral vein.

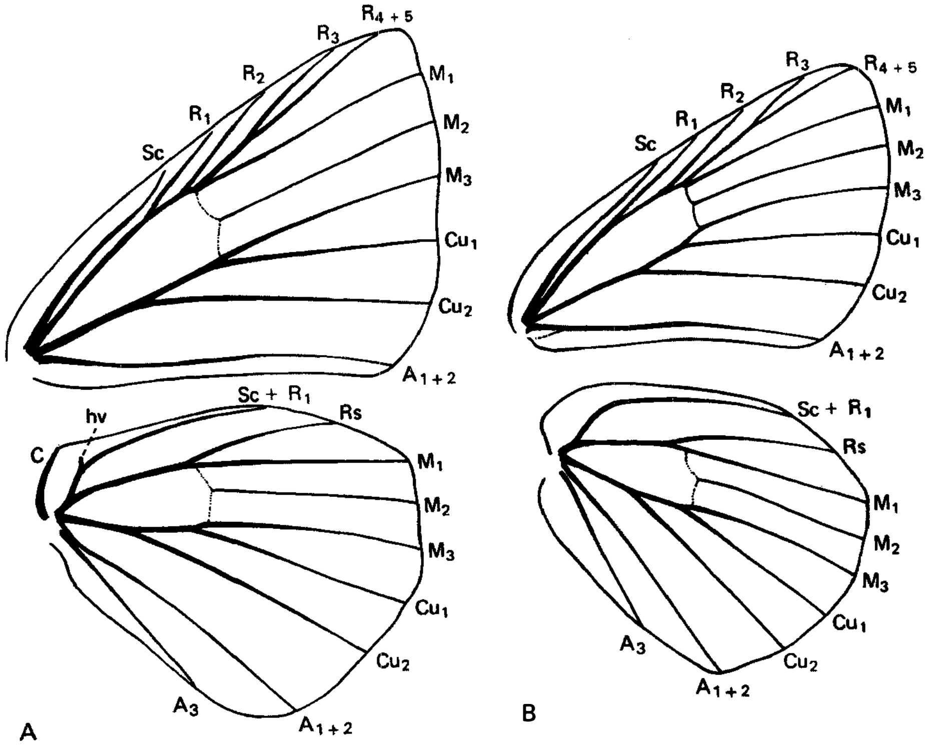

Figure 30–14 Wings of Lycaenidae. A, *Lephelisca* (Riodininae); B, *Lycaena* (Lycaeninae). *hv*, humeral vein.

8(7′).	Cubitus in front wing apparently 4-branched, hind wing with single anal vein (Figure 30–9); hind wing often with 1 or more tail-like prolongations on posterior margin	Papilionidae	p. 620
8′.	Cubitus in front wing apparently 3-branched, hind wing with 2 anal veins (Figures 30–10 through 30–14); hind wing usually without tail-like prolongations on posterior margin	9	
9(8′).	Labial palps very long, longer than thorax, and thickly hairy (Figure 30–61C)	Nymphalidae (Libytheinae)*	p. 623
9′.	Labial palps of normal size, shorter than thorax	10	
10(9′).	Radius in front wing 5-branched (Figures 30–10 through 30–12, 30–13A); front legs usually reduced in size	11	
10′.	Radius in front wing 3- or 4-branched (Figures 30–13B, 30–14, 30–60); front legs usually of normal size	14	
11(10).	A_3 in front wing present but short, A_{1+2} appearing to have a basal fork (Figure 30–10A); antennae not scaled above; relatively large, brownish or orange butterflies (Figure 30–65A)	Nymphalidae (Danainae)	p. 623
11′.	A_3 in front wing lacking, A_{1+2} not appearing forked at base (Figures 30–10B, 30–11, 30–12A, 30–13A); antennae usually scaled above	12	
12(11′).	Some veins in front wing (especially Sc) greatly swollen at base (Figure 30–10B); front wings more or less triangular; antennae swollen apically but not distinctly knobbed; small butterflies, usually brownish or grayish with eyespots in the wings (Figure 30–64)	Nymphalidae (Satyrinae)	p. 623
12′.	Generally with no veins in front wing greatly swollen at base (Sc in front wing slightly swollen in some Nymphalidae); wing color and shape, and antennae, usually not as in preceding entry	13	
13(12′).	M_1 in front wing stalked with R beyond discal cell (Figure 30–13A); front legs normal, or only slightly reduced, their claws bifid; small butterflies, usually white with black or orange markings (orange-tips)	Pieridae	p. 621
13′.	M_1 in front wing not stalked with R beyond discal cell; front legs much reduced, without tarsal claws, not used in walking; usually medium-sized to large butterflies, and not colored as in preceding entry	Nymphalidae (Nymphalinae)	p. 623
14(10′).	M_1 in front wing stalked with R beyond discal cell (Figure 30–13B); small to medium-sized butterflies, with white, yellow, or orange coloration, usually marked with black (Figure 30–59)	Pieridae	p. 621
14′.	M_1 in front wing usually not stalked with R beyond discal cell (Figure 30–14); usually not colored as in preceding entry	Lycaenidae	p. 622
15(6′).	Wings, especially hind wings, deeply cleft or divided into plumelike lobes (Figure 30–52); legs long and slender, with long tibial spurs	16	
15′.	Wings entire, or front wings only slightly cleft	17	
16(15).	Each wing divided into 6 plumelike lobes	Alucitidae*	p. 616
16′.	Front wings divided into 2–4 lobes, hind wings divided into 3 lobes (except *Agdistis*) (Figure 30–52)	Pterophoridae	p. 616
17(15′).	A part of the wings, especially hind wings, devoid of scales (Figure 30–46); front wings long and narrow, at least 4 times as long as wide (Figure 30–47); hind margin of front wings and costal margin of hind wings with a series of recurved and interlocking spines and wing folds; wasplike day-flying moths	Sesiidae	p. 612
17′.	Wings scaled throughout, or if with clear areas, then front wings are more triangular; wings without such interlocking spines	18	

18(17′).	Hind wings much broader than their fringe, usually wider than front wings, never lanceolate; tibial spurs variable, often short or absent	19	
18′.	Hind wings with fringe as wide as wings or wider, hind wings usually no wider than front wings, often lanceolate (Figure 30–42); tibial spurs long, more than twice as long as width of tibia	63	
19(18).	Hind wing with 3 anal veins behind discal cell	20	
19′.	Hind wing with 1–2 anal veins behind discal cell	31	
20(19).	Hind wing with Sc and Rs fused for a varying distance beyond discal cell or separate but very closely parallel (Figure 30–15); Sc and R in hind wing separate along front of discal cell, or base of R atrophied	Pyralidae, Crambidae	p. 617
20′.	Hind wing with Sc and Rs widely separate beyond discal cell, base of R usually well developed	21	
21(20′).	Sc and Rs in hind wing fused to near end of discal cell or at least fused beyond middle of cell (Figure 30–16)	22*	
21′.	Sc and Rs in hind wing separate from base or fused for a short distance along basal half of cell (Figures 30–17, 30–18)	23	
22(21).	Wings largely or wholly blackish, thinly scaled; R_5 in front wing arising from discal cell (Figure 30–16A)	Zygaenidae*	p. 612
22′.	Wings largely yellowish or white, densely clothed with soft scales and hair; R_5 in front wing stalked beyond discal cell (Figure 30–16B)	Megalopygidae*	p. 611
23(21′).	Front wing with an accessory cell (Figure 30–17A, acc)	24	
23′.	Front wing without an accessory cell (Figure 30–18)	27	
24(23).	Tibial spurs short, no longer than width of tibia; mouthparts often vestigial	25	
24′.	Tibial spurs long, more than twice as long as width of tibia; mouthparts usually well developed	63	

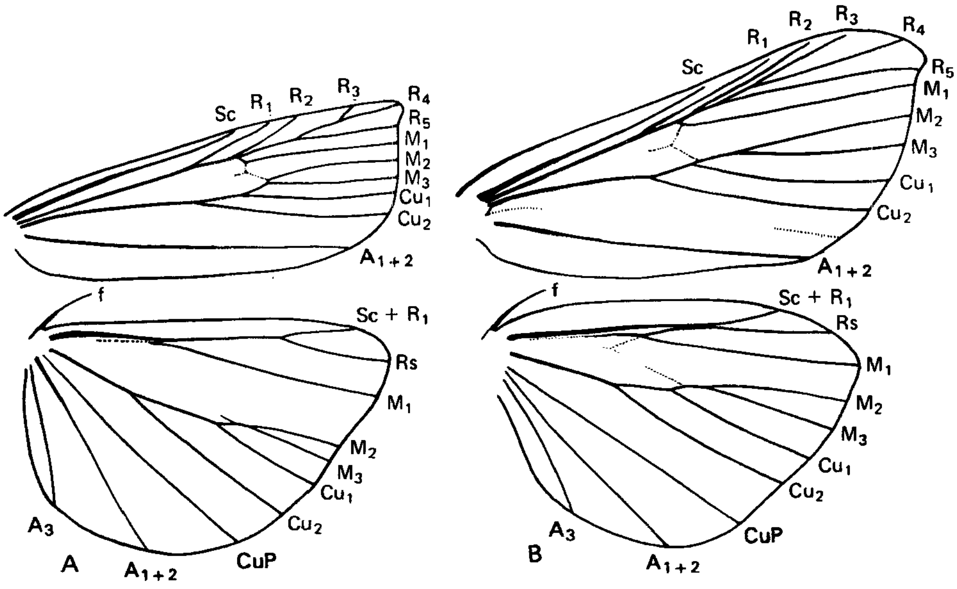

Figure 30–15 Wings of Pyraloidea. A, *Crambus* (Crambidae, Crambinae); B, *Pyralis* (Pyralidae, Pyralinae). *f*, frenulum.

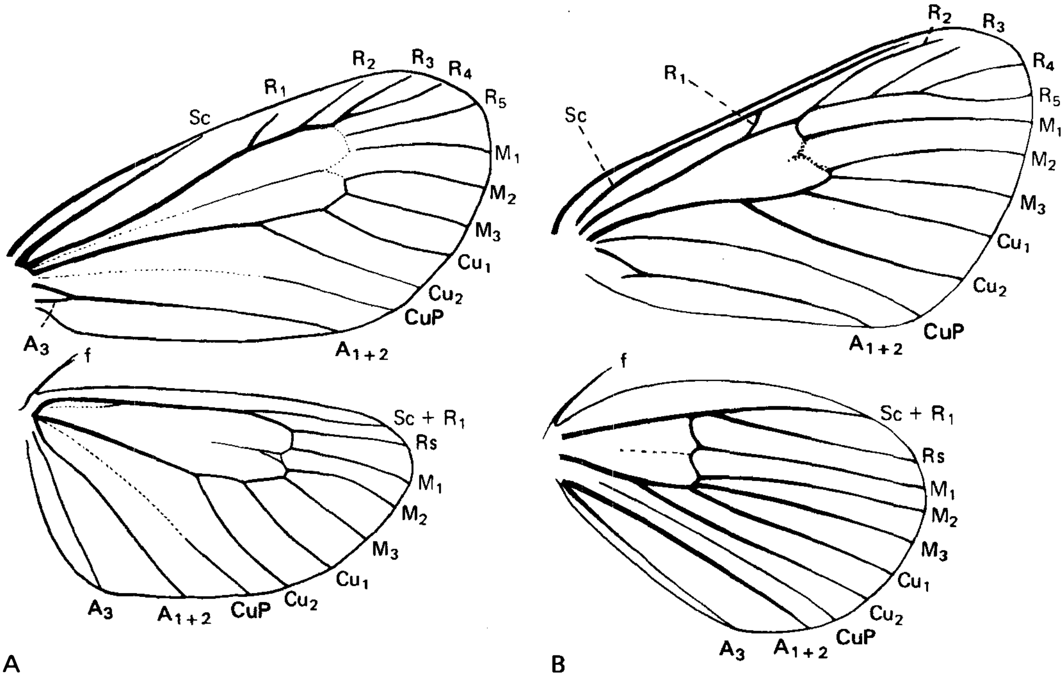

Figure 30–16 A, wings of *Malthaca* (Zygaenidae); B, wings of *Megalopyge* (Megalopygidae). *f*, frenulum.

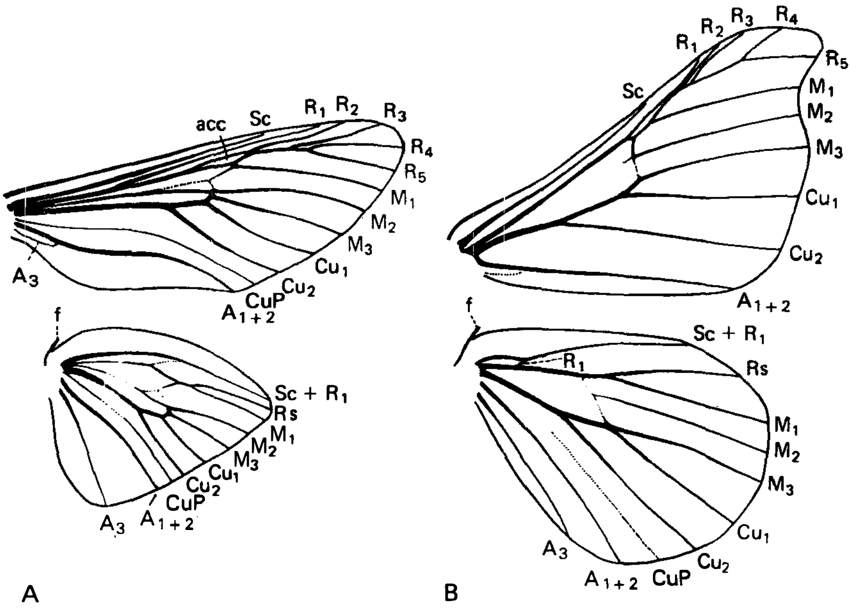

Figure 30–17 A, wings of *Prionoxystus* (Cossidae); B, wings of *Bombyx* (Bombycidae). *acc*, accessory cell; *f*, frenulum.

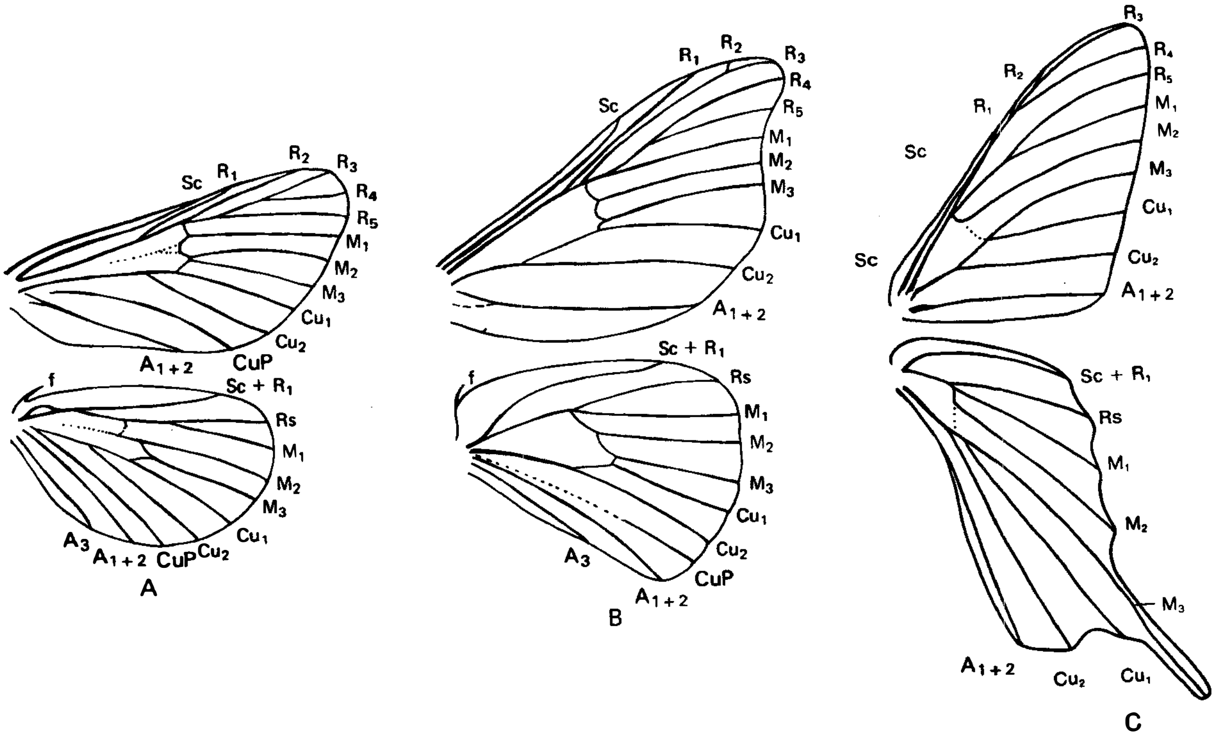

Figure 30–18 A, wings of *Euclea* (Limacodidae); B, wings of *Cicinnus* (Mimallonidae); C, wings of *Urania* (Uraniidae). *f*, frenulum.

25(24).	Front wing with some branches of R stalked, accessory cell extending beyond discal cell (Figure 30–17A)	26	
25′.	Front wing with no branches of R stalked, accessory cell not extending beyond discal cell; antennae bipectinate; small moths	Epipyropidae*	p. 611
26(25).	Front wings subtriangular, about one half longer than wide; wings densely clothed with soft scales and hair; Arizona	Dalceridae*	p. 612
26′.	Front wings more elongate, at least twice as long as wide; wings more thinly scaled; widely distributed	Cossidae*	p. 613
27(23′).	M_2 in front wing arising about midway between M_1 and M_3, or closer to M_1, cubitus appearing 3-branched (Figures 30–17B, 30–18B); frenulum present or absent	28*	
27′.	M_2 in front wing arising closer to M_3 than to M_1, cubitus appearing 4-branched; frenulum well developed (Figure 30–18A)	30	
28(27).	M_3 and Cu_1 in front wing stalked for a short distance beyond discal cell; frenulum well developed; California and Texas	Notodontidae (Dioptinae*)	p. 635
28′.	M_3 and Cu_1 in front wing not stalked beyond discal cell; frenulum small or absent; widely distributed	29*	
29(28′).	Front wing with R_{2+3} and R_{4+5} stalked independently of R_1; Sc and Rs in hind wing not connected by a crossvein (Figure 30–18B)	Mimallonidae*	p. 629
29′.	Front wing with R_2, R_3, R_4, and R_5 united on a common stalk; Sc and Rs in hind wing connected basally by a crossvein (R_1) (Figure 30–17B)	Bombycidae*	p. 631

30(27′).	CuP absent in front wing, well developed in hind wing	Copromorphidae*	p. 616
30′.	CuP weak in both front and hind wings, often developed only near wing margin (Figure 30–31A,B) (see also 30″)	Tortricidae	p. 613
30″.	CuP complete in both front and hind wings (Figure 30–18A)	Limacodidae	p. 612
31(19′).	Front wing with 2 distinct anal veins	32*	
31′.	Front wing with single complete anal vein (Figures 30–19B, 30–20 through 30–28) or with A_1 and A_2 fusing near tip or connected by a crossvein (Figure 30–19A)	33	
32(31).	Ocelli present; front wing 3 or more times as long as wide (*Harrisina*)	Zygaenidae*	p. 612
32′.	Ocelli absent; front wing not more than twice as long as wide	Hyblaeidae*	p. 616
33(31′).	Front wing with a single complete vein behind discal cell (A_{1+2}), CuP at most represented by a fold, A_3 absent or meeting A_{1+2} basally so that A_{1+2} appears forked at base (Figures 30–19B, 30–20 through 30–28)	34	
33′.	Front wing with A_1 and A_2 fusing near tip (Figure 30–19A) or connected by a crossvein	Psychidae	p. 606
34(33).	Antennae thickened, spindle-shaped (Figure 30–7C); Sc and Rs in hind wing connected by a crossvein near middle of discal cell, the 2 veins closely parallel to end of discal cell or beyond (Figure 30–19B); stout-bodied, often large moths (wingspread 50 mm or more) with narrow wings (Figure 30–77)	Sphingidae	p. 634
34′.	Antennae variable, rarely spindle-shaped; Sc and Rs in hind wing usually not connected by crossvein, or if such a crossvein is present, then the 2 veins strongly divergent beyond crossvein	35	
35(34′).	M_2 in front wing arising about midway between M_1 and M_3, cubitus appearing 3-branched (Figures 30–18B,C, 30–20 through 30–22), or (rarely) with M_2 and M_3 absent, cubitus appearing to have fewer than 3 branches	36	

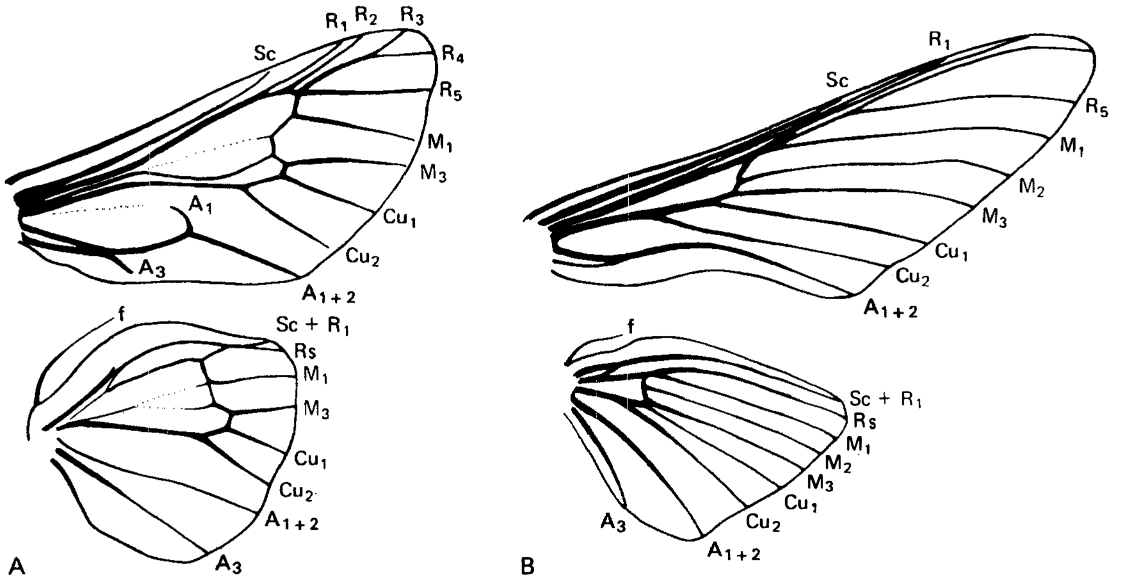

Figure 30–19 A, wings of *Thyridopteryx* (Psychidae); B, wings of *Hemaris* (Sphingidae). *f*, frenulum.

35′.	M_2 in front wing arising closer to M_3 than to M_1, cubitus appearing 4-branched (Figures 30–23 through 30–28)	49	
36(35).	Sc and Rs in hind wing swollen at base, fused to middle of discal cell, then diverging; M_2 and M_3 in front wing sometimes absent; small, slender moths	Arctiidae (Lithosiinae)	p. 640
36′.	Sc and Rs in hind wing not fused at base, although they may be fused farther distad or connected by a crossvein	37	
37(36′).	Antennae dilated apically; eyes hairy; Arizona	Sematuridae*	p. 628
37′.	Antennae not dilated apically, or if so, then eyes bare; widely distributed	38	
38(37′).	Sc in hind wing strongly angled at base, usually connected to humeral angle of wing by strong brace vein; beyond the bend Sc fuses with or comes close to Rs for a short distance along discal cell (Figure 30–20)	Geometridae	p. 628
38′.	Sc in hind wing straight or slightly curving at base, not of the configuration in preceding entry	39	
39(38′).	Frenulum well developed; Sc and Rs in hind wing variable	40	
39′.	Frenulum vestigial or absent; Sc and Rs in hind wing never fused but sometimes touching at a point beyond base or connected by a crossvein	45	
40(39).	Sc in hind wing widely separated from Rs from near base of wing; M_1 in front wing stalked with R_5, which is well separated from R_4	Uraniidae (Epipleminae)*	p. 628
40′.	Sc in hind wing close to Rs at least to middle of discal cell, often farther	41	

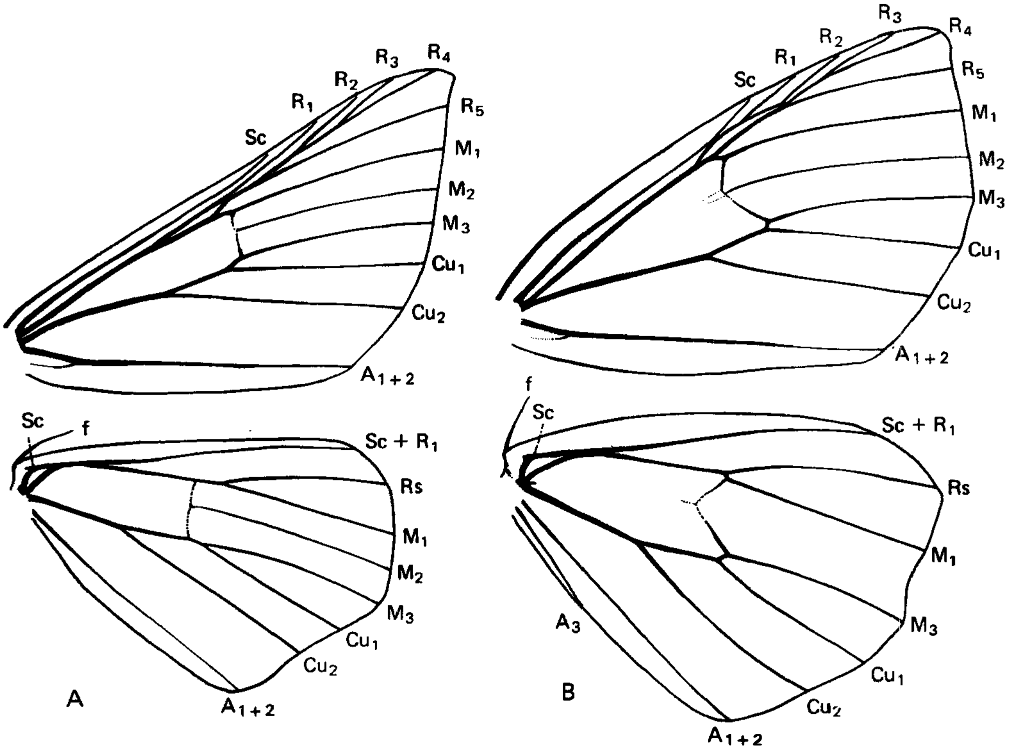

Figure 30–20 Wings of Geometridae. A, *Haematopsis*; B, *Xanthotype*. *f*, frenulum.

41(40′).	M_2 in hind wing arising nearer to M_3 than to M_1, cubitus appearing 4-branched; M_1 in hind wing arising from discal cell, not stalked with Rs beyond cell	Drepanidae (Thyatirinae)*	p. 627
41′.	M_2 in hind wing absent or arising midway between M_1 and M_3, or nearer to M_1, cubitus appearing 3-branched; M_1 in hind wing stalked with Rs for a short distance beyond discal cell (Figure 30–21)	42	
42(41′).	M_3 and Cu_1 in both front and hind wings stalked for a short distance beyond discal cell; slender, butterfly-like moths; California and Texas	Notodontidae (Dioptinae)*	p. 635
42′.	Not exactly fitting the description in preceding entry	43	
43(42′).	Slender-bodied moths; tympanal hood at base of abdomen; Sc sinuous or swollen at base	Geometridae*	p. 628
43′.	Stout-bodied moths; no tympanal hood at base of abdomen	44	
44(43′).	Sc and Rs in hind wing close together and parallel along almost entire length of discal cell (Figure 30–21B); proboscis usually present; front wings fully scaled; tarsal claws with blunt tooth at base	Notodontidae	p. 635
44′.	Sc and Rs in hind wing separating near middle of discal cell (Figure 30–21A); proboscis lacking; front wings with 1 or 2 small clear spots near tip; tarsal claws simple	Bombycidae (Apatelodinae)*	p. 631
45(39′).	Sc and Rs in hind wing connected by a crossvein (Figure 30–17B); white moths of medium size	Bombycidae*	p. 631
45′.	Sc and Rs in hind wing not connected by a crossvein (Figures 30–18B,C, and 30–21A); color variable, but not white; size medium to large	46	

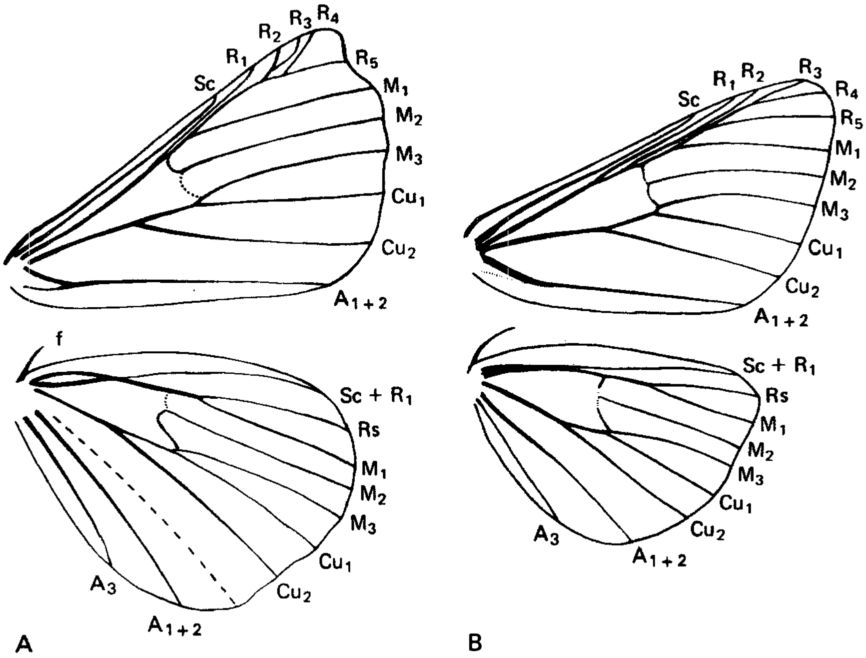

Figure 30–21 A, wings of *Apatelodes* (Bombycidae, Apatelodinae); B, wings of *Datana* (Notodontidae). *f*, frenulum.

46(45′).	Sc and Rs in hind wing separating near middle of discal cell, at the end of a long, narrow, basal areole; Rs and M_1 in hind wing stalked beyond discal cell (Figure 30–21A)	Bombycidae (Apatelodinae)*	p. 631
46′.	Sc and Rs in hind wing separating at base of wing; Rs and M_1 in hind wing not stalked beyond discal cell (Figures 30–18B,C, 30–22)	47	
47(46′).	M_2 in hind wing arising closer to M_1 than to M_3 (Figure 30–22); wingspread 25–150 mm	Saturniidae	p. 631
47′.	M_2 in hind wing arising about midway between M_1 and M_3 (Figure 30–18B,C); size variable	48*	
48(47′).	Hind wing with 1 anal vein (Figure 30–18C); large moths resembling a swallowtail butterfly; Texas	Uraniidae*	p. 628
48′.	Hind wing with 2 anal veins (Figure 30–18B); not swallowtail-like (Figure 30–70); widely distributed	Mimallonidae*	p. 629
49(35′).	All branches of R and M in front wing arising separately from the usually open discal cell (Figure 30–23A); wings generally with clear spots	Thyrididae*	p. 617
49′.	Front wing with some branches of R or M fused beyond discal cell (Figures 30–23B, 30–24 through 30–28)	50	
50(49′).	Hind wing with humeral veins, without frenulum; Cu_2 in front wing arising in basal half or third of discal cell (Figure 30–23B)	Lasiocampidae	p. 630
50′.	Hind wing without humeral veins, usually with frenulum; Cu_2 in front wing arising in distal half of discal cell	51	
51(50′).	Frenulum absent or vestigial; Sc and Rs in hind wing approximated, usually parallel along discal cell or fusing beyond middle of cell (Figure 30–24A); apex of front wings usually sickle-shaped	Drepanidae	p. 627

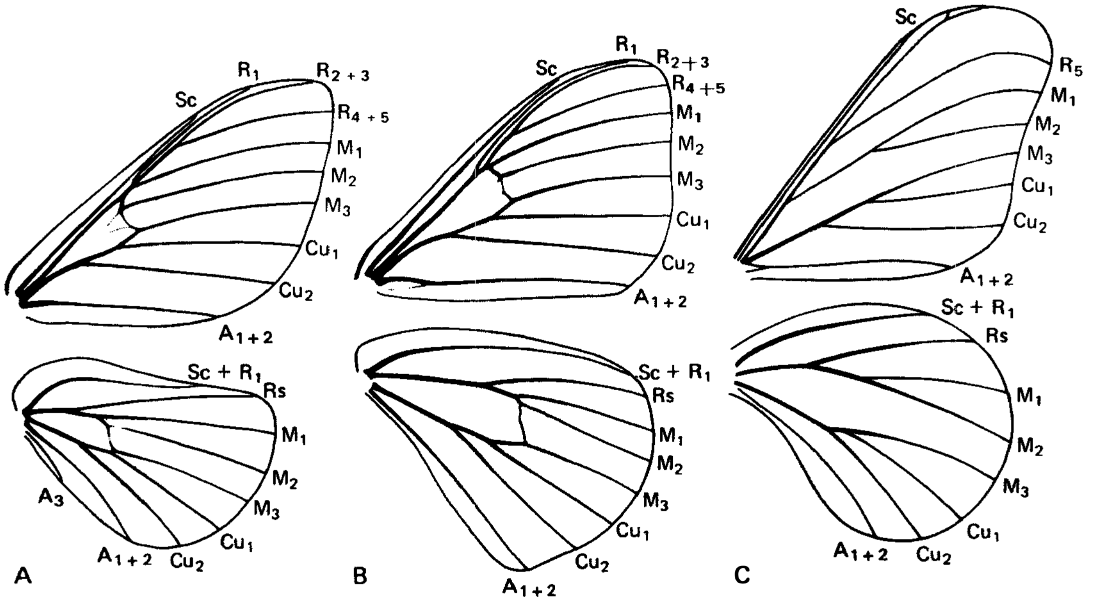

Figure 30–22 Wings of Saturniidae. A, *Anisota* (Ceratocampinae); B, *Automeris* (Hemileucinae); C, *Callosamia* (Saturniinae).

51′.	Frenulum well developed; Sc and Rs in hind wing not as in preceding entry; apex of front wings usually not sickle-shaped	52	
52(51′).	Antennae swollen apically; Sc in hind wing fused with Rs for only a short distance at base of discal cell (Figure 30–24B); ocelli present; moths with a wingspread of about 25 mm, usually black with white or yellow spots in wings (Figure 30–81)	Noctuidae (Agaristinae)	p. 636
52′.	Antennae usually not swollen apically; Sc in hind wing variable; ocelli present or absent	53	
53(52′).	Sc in hind wing apparently absent (Figure 30–25A); day-flying moths (Figure 30–82)	Arctiidae (Ctenuchinae)	p. 640
53′.	Sc in hind wing present and well developed	54	
54(53′).	Sc and Rs in hind wing fused for a varying distance beyond discal cell or separate but very closely parallel (Figure 30–15); Sc and Rs in hind wing separate along front of discal cell, or base of Rs atrophied	55*	
54′.	Hind wing with Sc and Rs widely separate beyond discal cell, base of Rs usually well developed	56	
55(54).	Front wings at least twice as long as wide, costal margin often irregular or lobed (if straight, M_2 and M_3 usually stalked); separation of Sc and Rs in hind wing generally well beyond discal cell; proboscis scaled; color variable, rarely white	Pyralidae (Chrysauginae)*	p. 617
55′.	Front wings less than twice as long as wide, costal margin straight; M_2 and M_3 not stalked; separation of Sc and Rs in hind wing about opposite end of discal cell; proboscis naked; white moths	Drepanidae (*Eudeilinea*)*	p. 627

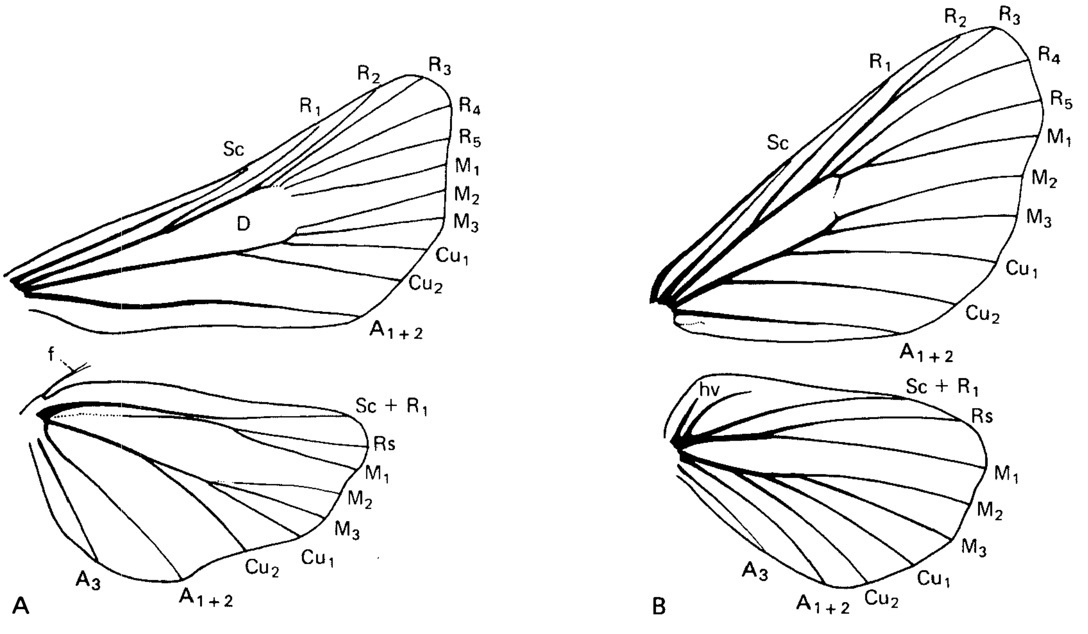

Figure 30–23 A, wings of *Thyris* (Thyrididae); B, wings of *Malacosoma* (Lasiocampidae). *f*, frenulum; *hv*, humeral veins.

56(54′).	Apex of front wings sickle-shaped (Figure 30–24A); Sc and Rs in hind wing separate, more or less parallel along anterior side of discal cell (as in Figure 30–24A)	**Drepanidae** (*Drepana*)*	p. 627
56′.	Apex of front wings not sickle-shaped; Sc and Rs in hind wing not as in preceding entry (Figure 30–25B), yellow spots or bands in wings, sometimes with metallic tints; Gulf states and western United States (Figures 30–26 through 30–28)	57	
57(56′).	Ocelli present	58	
57′.	Ocelli absent	60	
58(57).	Basal abdominal segment with 2 rounded, domelike elevations (tympanal hoods) dorsolaterally, occupying the length of the segment, separated by a distance equal to their width; M_3 and Cu_1 in hind wing usually stalked (Figure 30–25B); black or brownish moths with white or yellow spots or bands in wings, sometimes with metallic tints; Gulf states and western United States	Doidae*, Arctiidae (Arctiinae*)	pp. 635, 640
58′.	Tympanal hoods much smaller than in preceding entry or not apparent; M_3 and Cu_1 in hind wing not stalked; color variable; widely distributed	59	
59(58′).	Hind wing with Sc and Rs separating well before middle of discal cell, Sc not noticeably swollen at base; cubitus in hind wing appearing 3- or 4-branched (Figure 30–27); labial palps extending to middle of front or beyond; usually dark-colored moths	Pantheidae	p. 639

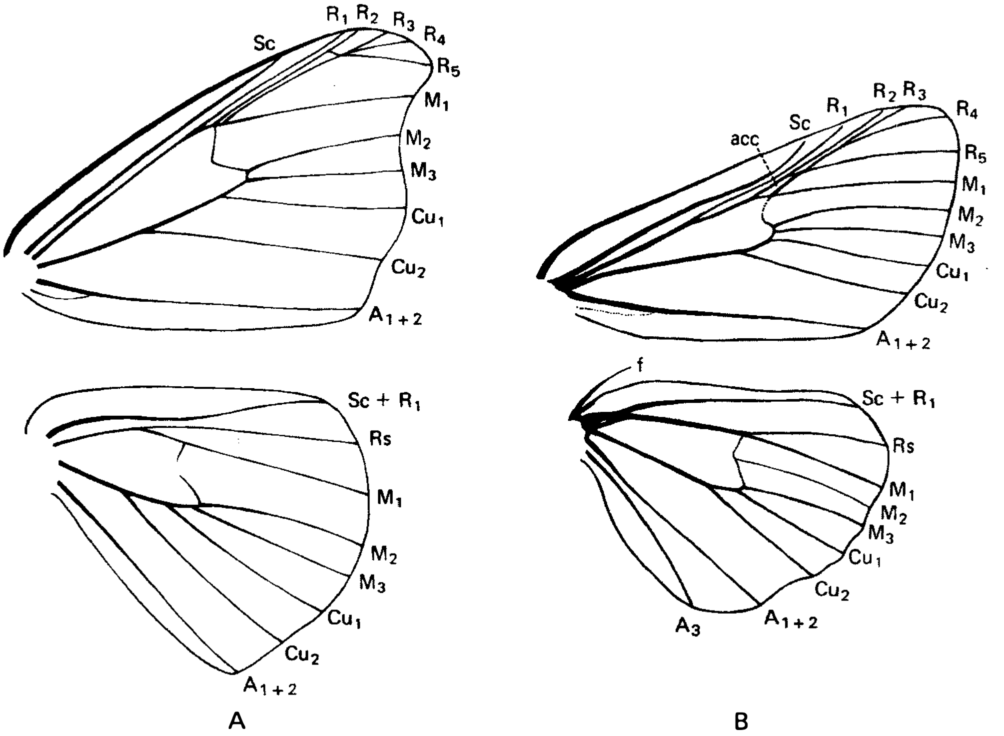

Figure 30–24 A, wings of *Oreta* (Drepanidae); B, wings of *Alypia* (Noctuidae, Agaristinae). *acc*, accessory cell; *f*, frenulum.

59′.	Hind wing with Sc and Rs usually fused (beyond a small basal areole) to middle of discal cell, or if not, then Sc swollen at base; cubitus in hind wing appearing 4-branched (Figure 30–26); labial palps not exceeding middle of front; usually light-colored moths	Arctiidae	p. 640
60(57′).	Front wings with tufts of raised scales; Sc and Rs in hind wing fused (beyond a small basal areole) to near middle of discal cell; small moths	Nolidae	p. 640
60′.	Front wings smoothly scaled; Sc and Rs in hind wing not as in preceding entry	61	
61(60′).	Hind wing with a relatively large basal areole, Sc and Rs fused for only a short distance at end of areole (Figure 30–28)	Lymantriidae	p. 639

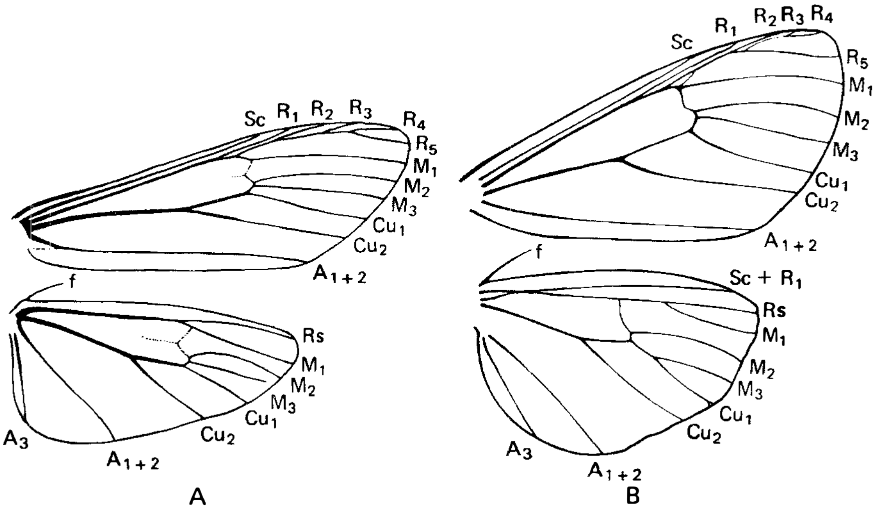

Figure 30–25 Wings of Arctiidae. A, *Cisseps* (Arctiinae, Ctenuchini); B, *Gnophaela* (Arctiinae, Pericopini). *f*, frenulum.

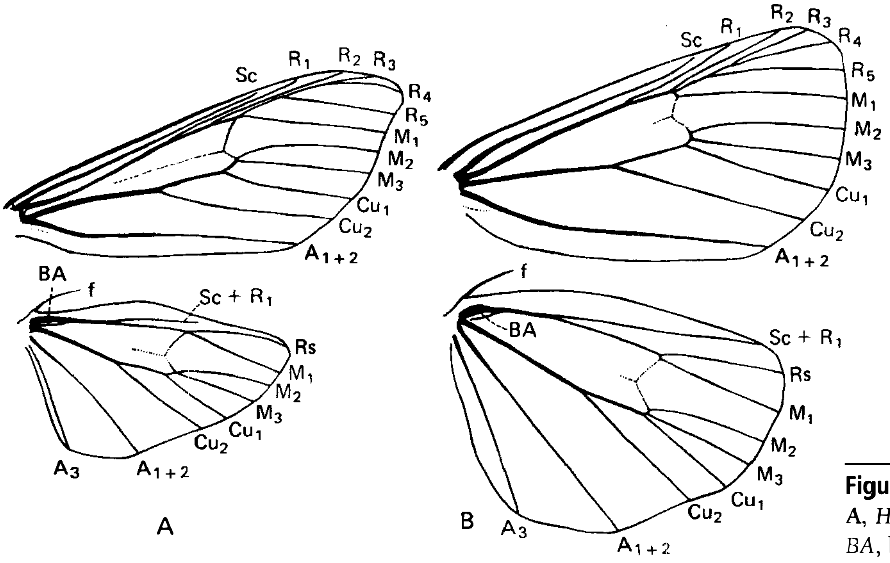

Figure 30–26 Wings of Arctiidae. A, *Halisidota*; B, *Apantesis*. *BA*, basal areole; *f*, frenulum.

61′.	Hind wing with very small basal areole or none, Sc and Rs fused for varying distance along discal cell, at most to middle of cell	62	
62(61′).	Labial palps short, usually not exceeding middle of face; size variable, wingspread up to about 40 mm; often brightly colored, reddish, yellowish, or white	Arctiidae (Lithosiinae)	p. 640
62′.	Labial palps longer, extending to middle of face or beyond; wingspread 20 mm or less; dull-colored moths.	Noctuidae (Strepsimaninae)*	p. 636
63 (18′,24′).	Basal segment of antennae enlarged, concave beneath, forming an eye cap (Figure 30–29B)	64	

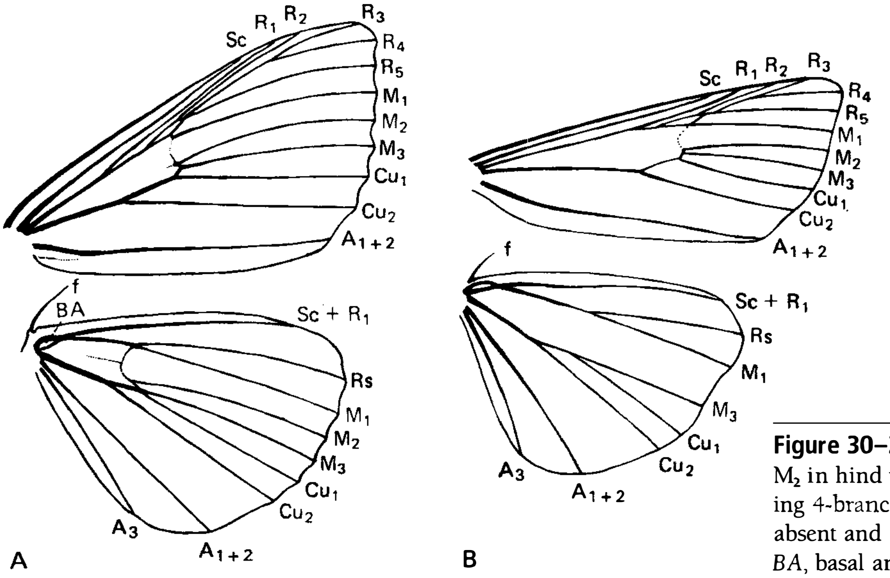

Figure 30–27 Wings of Noctuidae, with M_2 in hind wing present and Cu appearing 4-branched (A), and M_2 in hind wing absent and Cu appearing 3-branched (B). *BA*, basal areole.

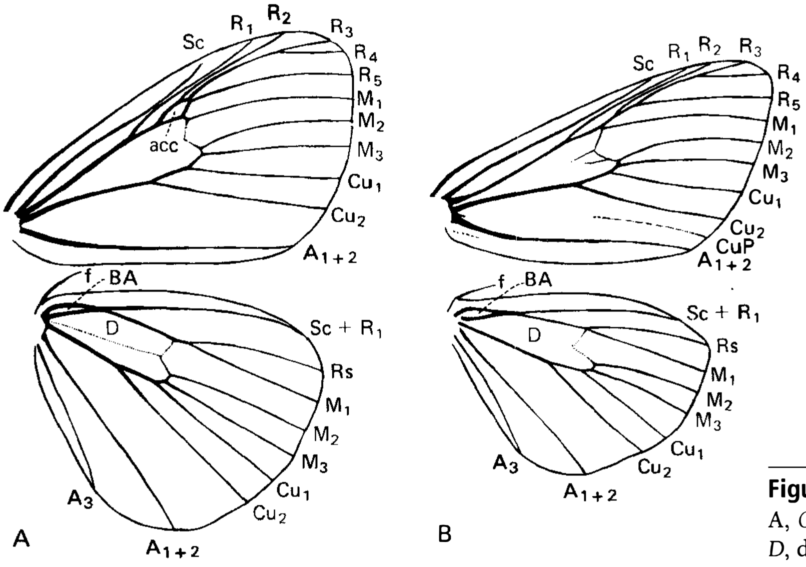

Figure 30–28 Wings of Lymantriidae. A, *Orgyia*; B, *Lymantria*. *BA*, basal areole; *D*, discal cell; *f*, frenulum.

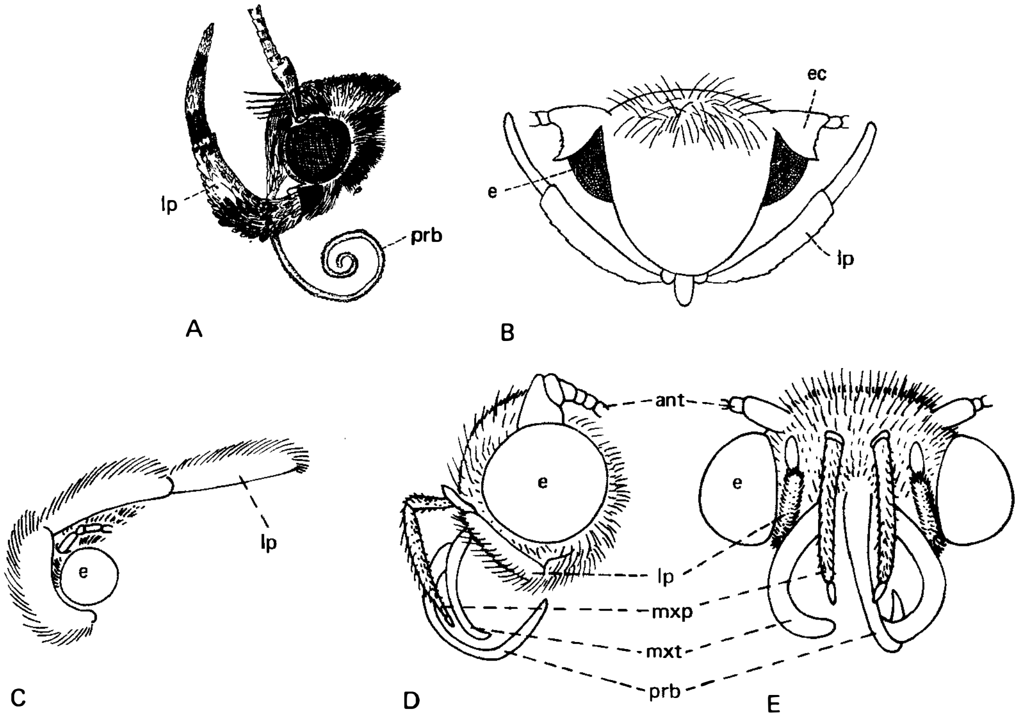

Figure 30–29 Head structure in microlepidoptera. A, *Pectinophora* (Gelechiidae), lateral view; B, *Zenodochium* (Coleophoridae, Blastobasinae), anterior view; C, *Acrolophus* (Acrolophidae), lateral view; D, lateral, and E, anterior views of *Tegeticula* (Prodoxidae). *ant*, antenna; *e*, compound eye; *ec*, eye cap; *lp*, labial palp; *mxp*, maxillary palp; *mxt*, maxillary tentacle; *prb*, proboscis. (A, redrawn from Busck; B, redrawn from Dietz.)

63′.	Basal segment of antennae not forming an eye cap (Figure 30–29A)	68	
64(63).	Maxillary palps well developed, conspicuous; wing membrane aculeate (with minute spines under scales); proboscis scaled	65*	
64′.	Maxillary palps vestigial; wing membrane not aculeate; proboscis naked (except Blastobasinae)	66	
65(64).	Front wing with only 3 or 4 unbranched veins; wingspread usually over 3 mm; often white	Opostegidae*	p. 604
65′.	Front wing with branched veins (Figure 30–30A); wingspread 3 mm or less; often with metallic bands	Nepticulidae*	p. 604
66(64′).	Labial palps minute and drooping, or absent; ocelli absent	Bedellidae*, Bucculatricidae, Lyonetiidae*	pp. 608, 606, 608
66′.	Labial palps of at least moderate size, upcurved or projecting forward; ocelli present or absent	67	
67(66′).	Wings pointed at apex; hind wing without discal cell; veins beyond discal cell in front wing diverging; no stigmalike thickening in front wing between C and R_1; proboscis naked (*Phyllocnistis*, etc.)	Gracillariidae	p. 606

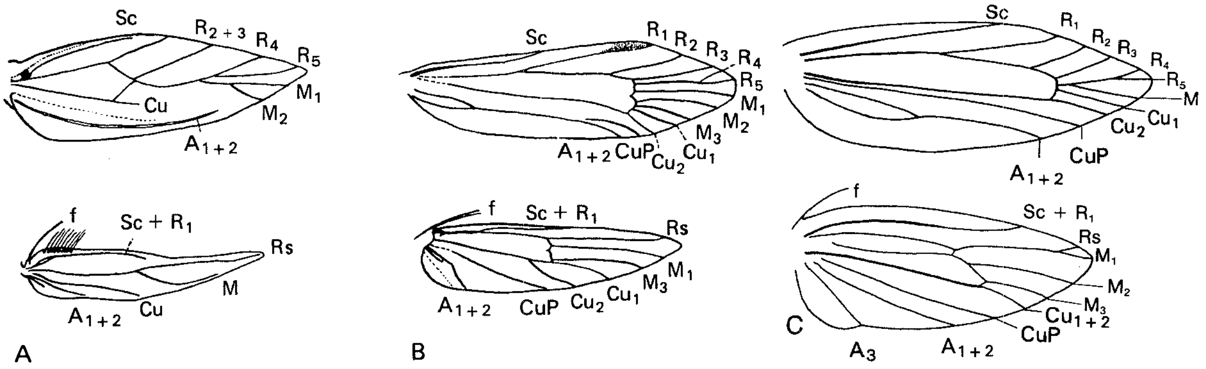

Figure 30–30 Wings of microlepidoptera. **A**, *Obrussa* (Nepticulidae); **B**, *Holcocera* (Coleophoridae, Blastobasinae); **C**, *Ochsenheimeria* (Ypsolophidae, Ochsenheimeriinae). *f*, frenulum. (**A**, redrawn from Braun; **B**, redrawn from Comstock 1975 after Forbes, by permission of Comstock Publishing Co.; **C**, redrawn from Davis.)

67′.	Wings more or less rounded at apex; hind wing usually with a closed cell; veins beyond discal cell in front wing nearly parallel; front wing with stigmalike thickening between C and R_1 (as in Figure 30–30B); proboscis scaled	Coleophoridae (Blastobasinae: *Calosima*)*	p. 609
68(63′).	Maxillary palps well developed, folded in a resting position (Figure 30–29D,E)	69	
68′.	Maxillary palps vestigial or, if present, projecting forward in a resting position	73	
69(68).	Head smooth-scaled; R_5, when present, extending to costal margin of wing; strongly flattened moths; southern United States, Florida to California	Tineidae (Hieroxestinae)*	p. 605
69′.	Head tufted, at least on vertex, or R_5 extending to outer margin of wing; widely distributed	70	
70(69′).	R_5 in front wing extending to costal margin of wing or absent	71	
70′.	R_5 in front wing extending to outer margin of wing	Acrolepiidae*	p. 608
71(70).	Wing membrane aculeate (see couplet 64); antennae smooth, often very long; female with piercing ovipositor	72	
71′.	Wing membrane not aculeate; antennae usually rough, with a whorl of erect scales on each segment; ovipositor membranous, retractile	Tineidae	p. 605
72(71).	Folded part of maxillary palps about half as long as width of head; dark-colored moths	Incurvariidae*	p. 605
72′.	Folded part of maxillary palps about two thirds as long as width of head; mostly whitish moths	Prodoxidae	p. 604
73(68′).	First segment of labial palps as large as second or larger, palps recurved back over head and thorax (Figure 30–29C); ocelli absent; proboscis vestigial or absent; moderate-sized, stout, noctuid-like moths with eyes hairy	Acrolophidae	p. 605
73′.	Without the combination of characters in preceding entry	74	
74(73′).	Distal margin of hind wings concave, apex produced (Figure 30–31C); proboscis scaled	Gelechiidae	p. 610

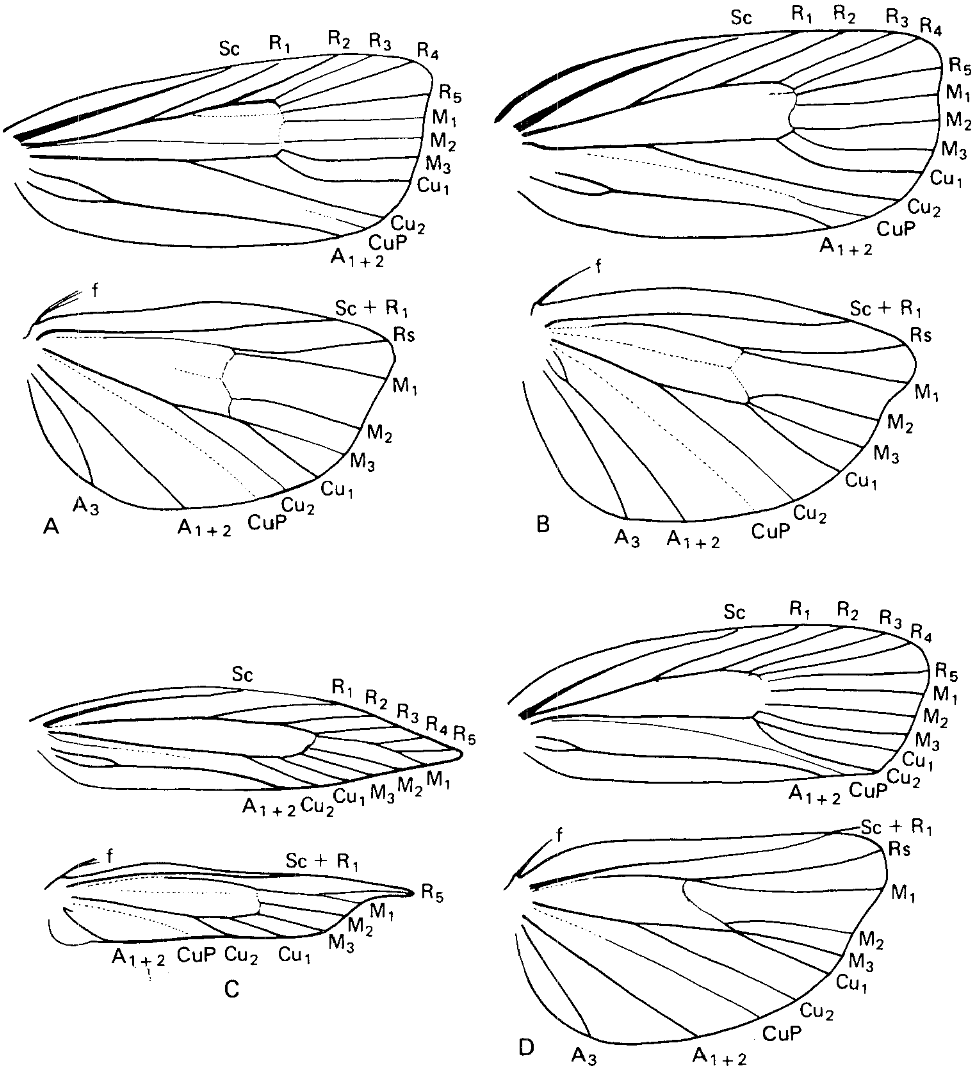

Figure 30–31 Wings of microlepidoptera. A, and B, Tortricidae; C, Gelechiidae; D, Elachistidae (*Stenoma*, Stenomatinae). *f*, frenulum.

74′. Hind wings with distal margin rounded or trapezoidal, anal region well developed, venation complete or nearly so (Figures 30–31A,B,D, 30–32); proboscis scaled or naked (see also 74″) 75

74″. Wings lanceolate or linear, pointed or narrowly rounded at apex, anal region and venation often reduced (Figures 30–33, 30–34A) 90

75(74′). CuP in front wing lacking 76*

75′. CuP present in front wing, at least apically 78

76(75). Third segment of labial palps short and blunt, palps beaklike; R_5 rarely stalked with R_4, usually extending to outer margin of wing (Cochylinae) Tortricidae p. 613

76′. Third segment of labial palps long and slender, usually tapering, palps generally upturned to middle of front or beyond; R_5 in front wing usually stalked with R_4, extending to costal margin of wing 77*

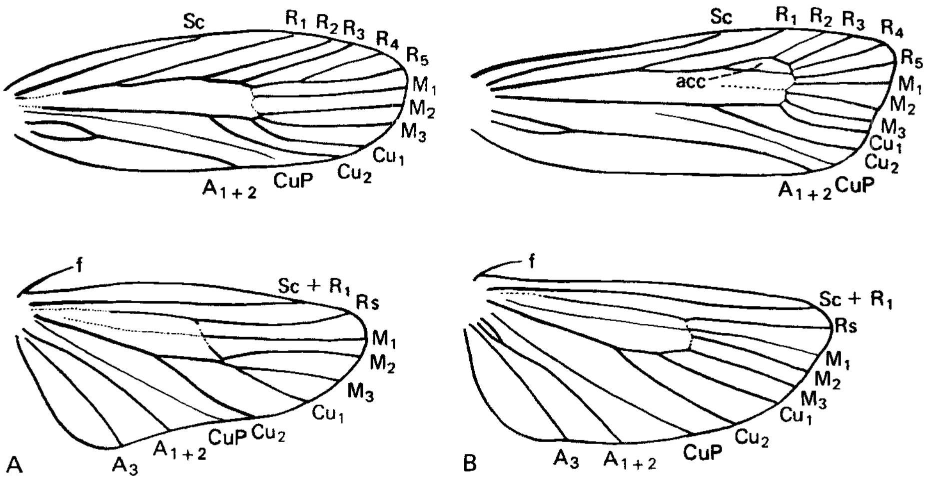

Figure 30–32 Wings of microlepidoptera. A, *Depressaria* (Elachistidae, Depressariinae); B, *Atteva* (Yponomeutidae). *acc*, accessory cell; *f*, frenulum.

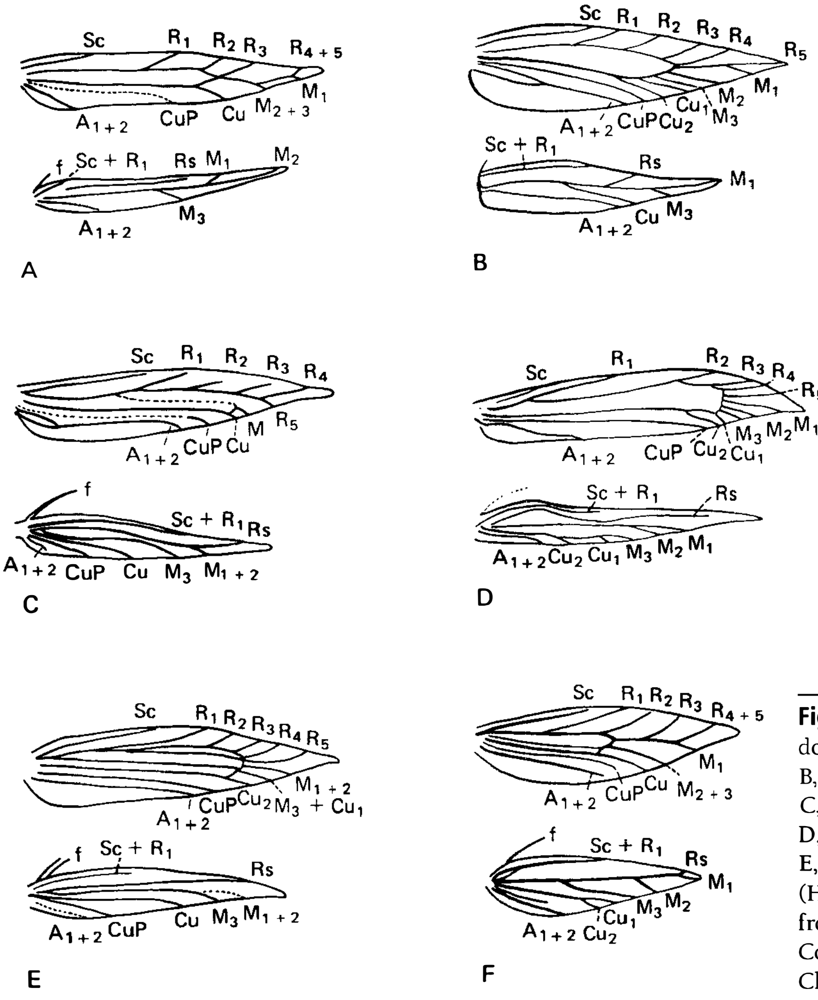

Figure 30–33 Wings of microlepidoptera. A, *Bedellia* (Bedellidae); B, *Tinagma* (Douglasiidae); C, *Coleophora* (Coleophoridae); D, *Gracillaria* (Gracillariidae); E, *Tischeria* (Tischeriidae); F, *Antispila* (Heliozelidae). *f*, frenulum. (Redrawn from Comstock, by permission of the Comstock Publishing Co.; A, after Clemens; E and F, after Spuler.)

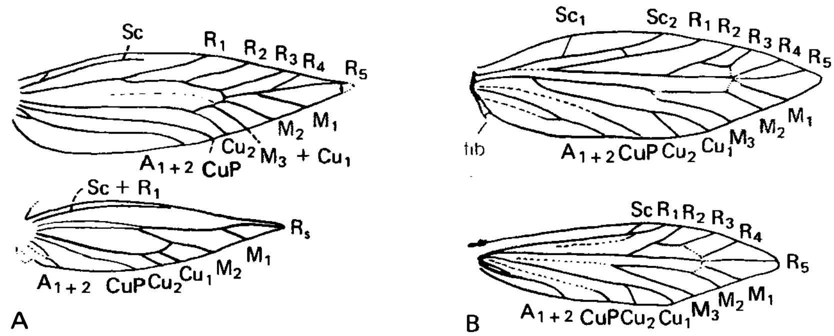

Figure 30–34 Wings of Lepidoptera. A, *Elachista* (Elachistidae); B, *Micropteryx* (Micropterigidae). *fib*, fibula. (Redrawn with permission from Comstock, J. H. 1940. *An introduction to entomology,* 9th ed. Ithaca, NY: Comstock Publishing Company.)

77(76′).	Hind wing with all 3 branches of M present	Copromorphidae*	p. 616
77′.	Hind wing with M only 1- or 2-branched	Carposinidae*	p. 616
78(75′).	Front wing with A_3 meeting A_{1+2} near its middle; Cu_2 arising at apex of discal cell, appearing as a continuation of the Cu stem, M unbranched, R_{4+5} stalked (Figure 30–30C); northeastern United States	Ypsolophidae (Ochsenheimeriinae)*	p. 607
78′.	Front wing with A_3 meeting A_{1+2} near its base, Cu_2 not as in preceding entry, M usually 2- or 3-branched, R_{4+5} variable; widely distributed	79	
79(78′).	Cu_2 in front wing arising in basal three fourths of discal cell (Figure 30–31A,B); third segment of labial palps short and blunt, little if any longer than wide	Tortricidae	p. 613
79′.	Cu_2 in front wing usually arising in distal fourth of discal cell (Figure 30–31D); labial palps variable, but third segment usually long and slender	80	
80(79′).	Labial palps and proboscis well developed	81	
80′.	Labial palps and proboscis vestigial (*Solenobia*)	Psychidae*	p. 606
81(80).	Vertex and upper part of face tufted with dense bristly hairs	82	
81′.	Upper face (and usually also vertex) smooth, with short scales	83	
82(81).	Wing membrane aculeate (see couplet 64); antennae longer than wings in male; female with piercing ovipositor; day-flying	Adelidae*	p. 604
82′.	Wing membrane usually not aculeate; antennae generally short; female with ovipositor membranous and retractile; generally nocturnal	Tineidae	p. 604
83(81′).	Rs and M_1 in hind wing arising close together, stalked or fused (Figure 30–31D)	84*	
83′.	Rs and M_1 in hind wing well separated at their origin, at least half as far apart as at wing margin (Figure 30–32)	85	
84(83).	Front wings narrowly rounded or pointed apically (*Cerostoma*)	Ypsolophidae*	p. 607
84′.	Front wings broadly rounded or blunt apically (Figure 30–31D)	Elachistidae	p. 608
85(83′).	Ocelli very large and conspicuous	86*	
85′.	Ocelli small or absent	87	
86(85).	Costa strongly arched; hind wings rounded, only slightly longer than wide; proboscis scaled basally	Choreutidae*	p. 615
86′.	Costa not strongly arched; hind wings usually more or less elongate, distinctly longer than wide; proboscis naked	Glyphipterigidae*	p. 608
87(85′).	R_4 and R_5 in front wing stalked; proboscis scaled	88*	
87′.	R_4 and R_5 in front wing not stalked; proboscis naked	89	

88(87).	Front wing with stigmalike thickening between C and R_1 (Figure 30–30B); hind wings narrower than front wings	Coleophoridae (Blastobasinae)	p. 609
88′.	Front wing without such a stigmalike thickening; hind wings usually as wide as front wings (Figure 30–32A)	Elachistidae (Depressariinae), Amphisbatidae, Peleopodidae*	p. 608, 610, 610
89(87′).	M_1 and M_2 in hind wing stalked	110*	
89′.	M_1 and M_2 in hind wing not stalked	Urodidae*, Yponomeutidae	p. 615, 607
90(74″).	Face and vertex with long, bristly hairs; antennae usually rough, with 1 or 2 whorls of erect scales on each segment; ocelli absent	Tineidae	p. 605
90′.	Face smooth-scaled; antennae variable; ocelli present or absent	91	
91(90′).	Front wing with closed discal cell	92	
91′.	Front wing without closed discal cell	115*	
92(91).	Hind wing without discal cell, with R stem near middle of wing (well separated from Sc) and with a branch extending to C at about three fifths the wing length (Figure 30–33B); R_5 in front wing free from R_4 but stalked with M_1; labial palps stout and drooping	Douglasiidae*	p. 606
92′.	Not exactly fitting the description in preceding entry	93	
93(92′).	Discal cell in front wing somewhat oblique, its apex closer to hind margin of wing than to front margin, branches of Cu very short (Figure 30–33C)	94	
93′.	Discal cell in front wing not oblique, its apex not much closer to hind margin of wing than to front margin, branches of Cu longer (Figures 30–30B, 30–33D,F, 30–34A)	96*	
94(93).	Front wing with stigmalike thickening between C and R_1 (Figure 30–30B); scape of antenna with a row of long hairs	Coleophoridae (Blastobasinae)	p. 609
94′.	Front wing without such a stigmalike thickening; scape of antenna variable	95	
95(94′).	Front tibiae slender, epiphysis apical or absent; antennae turned forward at rest	Coleophoridae	p. 609
95′.	Front tibiae stout, epiphysis well developed, at middle of tibia; antennae turned backward at rest	Batrachedridae*, Cosmopterigidae*, Coleophoridae (Momphinae)	p. 609, 610, 609
96(93′).	Front wing with 5 veins reaching costal margin beyond Sc	97*	
96′.	Front wing with 4 or fewer veins reaching costal margin beyond Sc	107*	
97(96).	Accessory cell in front wing large, at least half as long as discal cell (Figure 30–33E); vertex with a flat tuft covering base of antennae	Tischeriidae*	p. 605
97′.	Accessory cell in front wing smaller, less than half as long as discal cell, or absent; vertex usually not as in preceding entry	98*	
98(97′).	Vertex more or less tufted, or with rough, bristly hair (*Parornix*)	Gracillariidae*	p. 606
98′.	Vertex smooth-scaled	99*	
99(98′).	R_1 in front wing arising basad of middle of discal cell, usually at about basal third (Figure 30–33D,E)	100*	
99′.	R_1 in front wing arising at or beyond middle of discal cell (Figures 30–30B, 30–33F, 30–34A)	102*	
100(99).	Front wing with stigmalike thickening between C and R_1 (Figure 30–30B); R_4 and R_5 stalked	Coleophoridae (Blastobasinae)	p. 609
100′.	Front wing without such a stigmalike thickening, R_4 and R_5 usually not stalked (Figure 30–33D)	101*	

101(100′).	Third segment of labial palps pointed; maxillary palps folded over base of proboscis	Cosmopterigidae (*Limnaecia, Stagmatophora, Anoncia*)*	p. 610
101′.	Third segment of labial palps usually blunt; maxillary palps projecting forward, rudimentary, or absent	Gracillariidae*	p. 606
102(99′).	Front wing with R_1 arising distinctly beyond middle of discal cell, M unbranched; venation of hind wing much reduced; tip of front wing drawn out to a narrow point	Gracillariidae*	p. 606
102′.	Front wing with R_1 arising at about middle of discal cell, M usually 2- or 3-branched; venation of hind wing usually complete; tip of front wing not as in preceding entry	103*	
103(102′).	Hind tarsi with more or less distinct groups of bristles near ends of segments; labial palps usually short, sometimes drooping; proboscis naked	Schreckensteiniidae*	p. 616
103′.	Hind tarsi without such bristles; labial palps long, upcurved, third segment long and tapering; proboscis scaled	104*	
104(103′).	R_4 and R_5 in front wing stalked	105*	
104′.	R_4 and R_5 in front wing not stalked	106*	
105(104).	Hind wings lanceolate, with complete venation (*Borkhausenia*)	Oecophoridae*	p. 609
105′.	Hind wings usually linear, with venation reduced	Cosmopterigidae*	p. 610
106(104′).	Several veins arising from end of discal cell between continuation of R and Cu stems	Elachistidae (Agonoxeninae)*	p. 608
106′.	No veins emerging from end of discal cell between continuation of R and Cu stems	Gelechiidae (*Helice, Theisoa*, etc.)*	p. 610
107(96′).	Venation of front wing reduced, with 7 or fewer veins reaching wing margin from discal cell (Figure 30–33F)	108*	
107′.	Venation of front wing complete or nearly so, with 8–10 veins reaching wing margin from discal cell	109*	
108(107).	Vertex rough-scaled	Gracillariidae (*Cremastobombycia, Phyllonorycter = Lithocolletis*)*	p. 606
108′.	Head entirely smooth-scaled	Heliozelidae*	p. 604
109(107′).	Vertex more or less tufted; M_1 and M_2 in hind wing stalked	110*	
109′.	Vertex smooth; usually no branches of M in hind wing stalked	111*	
110(89,109).	Ocelli present	Galacticidae*, Plutellidae*	p. 615, 608
110′.	Ocelli absent	Yponomeutidae (Argyresthiinae)*	p. 607
111(109′).	R_1 in front wing arising at about two thirds the length of discal cell; 9 veins in front wing reaching margin from discal cell	Xyloryctidae (Scythridinae)*	p. 609
111′.	R_1 in front wing usually arising near middle of discal cell or more basad; 8–10 veins in front wing reaching margin from discal cell	112*	
112(111′).	Labial palps long, upturned (as in Figure 30–29A); venation of front wing usually complete, with 10 veins reaching margin from discal cell	113*	
112′.	Labial palps shorter, of moderate size or small, slightly upturned; venation of front wing somewhat reduced, with only 8 or 9 veins reaching margin from discal cell	114*	

113(112).	Hind tibiae stiffly bristled, usually in tufts at the spurs; ocelli absent; proboscis naked	Epermeniidae*	p. 616
113′.	Hind tibiae without such bristles; ocelli present or absent; proboscis scaled	Elachistidae (Agonoxeninae*), Coleophoridae (Momphinae*), Cosmopterigidae*	p. 608, 610
114(112′).	Front wing with only 1 or 2 veins arising from apex of discal cell; hind wing with forked vein at apex (Figure 30–34A); proboscis scaled	Elachistidae*	p. 608
114′.	Front wing with at least 3 veins arising from apex of discal cell; hind wing without forked vein at apex; proboscis naked	Heliodinidae*	p. 608
115(91′).	Front wings linear, with only 3 or 4 veins	Heliodinidae (*Cycloplasis*)*	p. 608
115′.	Front wings lanceolate, with 7 veins reaching margin	Heliozelidae (*Coptodisca*)*	p. 604
116(1′).	Moth developing in, and usually never leaving, a sac or case constructed and carried about by the larva	Psychidae	p. 606
116′.	Moth not developing in a sac or case constructed by the larva	117	
117(116′).	Ocelli present	118*	
117′.	Ocelli absent	119	
118(117).	Proboscis present and naked; maxillary palps short, almost concealed; not aquatic	Tortricidae*	p. 613
118′.	Proboscis small and scaled or vestigial; maxillary palps large; wings very small; aquatic moths	Crambidae (Nymphulinae, *Acentria*)*	p. 617
119(117′).	Stout-bodied, short-legged, usually densely woolly; proboscis absent or vestigial	Lymantriidae	p. 639
119′.	Slender-bodied, long-legged, hairy or scaly; proboscis present	Geometridae	p. 628

SUPERFAMILY **Micropterigoidea:** These moths differ from other Lepidoptera in having mandibulate mouthparts, with the mandibles well developed and the galeae short and not forming a proboscis. The venation of the front and hind wings is similar, and a fibula is present (Figure 30–34B). The larvae have eight pairs of short, conical prolegs, each bearing a single claw.

Family **Micropterigidae—Mandibulate Moths:** This is a small group, with only two North American species, and its members are seldom encountered. One species *Epimartyria auricrinella* (Walsingham), which has a wingspread of about 8 mm, occurs in the East. The larvae feed on mosses and liverworts, and the adults feed on pollen.

SUPERFAMILY **Eriocranioidea:** These moths resemble the Micropterigidae in having the venation of the front and hind wings similar. The middle tibiae bear a single spur (none in Micropterigidae). The females have a horny, piercing ovipositor. There is a single genital opening in the female, behind the ninth sternum. Pupation occurs in the ground, and the pupae (which are exarate) have well-developed mandibles with which they chew their way out of the cocoon. The larvae are leaf miners. The adults have vestigial mandibles.

Family **Eriocraniidae:** These are small moths (wingspread 6.0–13.5 mm) that are similar to clothes moths in general appearance, but they have metallic markings in the wings. One of the best-known eastern species in this family is *Dyseriocrania auricyanea* (Walsingham). Its larvae make blotch mines in oak and chestnut and overwinter as pupae in the soil. The moths in this family typically fly very early in the year—February in north Florida and late March in Virginia.

Family **Acanthopteroctetidae:** These moths resemble the Eriocraniidae, but can be differentiated by the characters given in the key (couplet 5). This family was established by Davis (1978a), with four known species in the western states from northwestern Montana to southern California. *Acanthopteroctetes unifascia* Davis is a leaf miner in *Ceanothus* (Rhamnaceae).

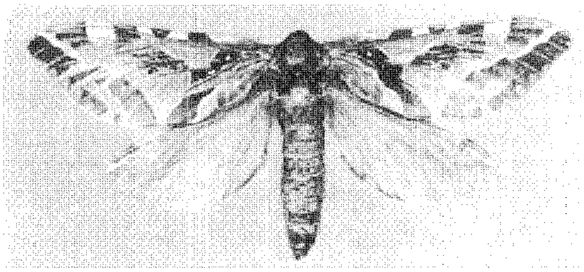

Figure 30–35 A hepialid moth, *Sthenopis argenteomaculatus* Harris, .9×.

SUPERFAMILY Hepialoidea: These moths have similar venation in the front and hind wings, and have a well-developed jugum (Figure 30–5). The female has two genital openings, but that of the corpus bursae is very close to the egg pore on segment 9. The larvae are root borers.

***Family* Hepialidae—Ghost Moths and Swifts:** These are medium-sized to large moths, with wingspreads of 25–75 mm. Most are brown or gray with silvery spots in the wings (Figure 30–35). The name "swift" refers to the fact that some of these moths have an extremely rapid flight. They superficially resemble some of the Sphingidae. The smaller moths in this family, with wingspreads of 25–50 mm, belong to the genera *Gazoryctria* and *Korscheltellus*. Most of their larvae bore in the roots of herbaceous plants. The larger hepialids belong to the genus *Sthenopis*. The larva of *S. argenteomaculatus* (Harris) (Figure 30–35) bores in the roots of alder, and that of *S. thule* Strecker bores in the roots of willows.

GROUP Monotrysia: Sometimes considered a suborder, this group comprises the three superfamilies Nepticuloidea, Incurvarioidea, and Tischerioidea. Females have a single genital opening, located on segment 9. The venation of the front and hind wings is different (RS is branched in the front wing, but not in the hind wing); a frenulum is present, and the wings are aculeate (except in the Heliozelidae).

SUPERFAMILY Nepticuloidea: In the adults of this group, the antennal scape is expanded and covers the eye. The cell of the fore wing is open.

***Family* Nepticulidae:** The Nepticulidae are minute moths, some species of which have a wingspread of only 3 mm. More than 80 species are known for North America. The wing venation is somewhat reduced, and the surface of the wings bears spinelike hairs or aculeae. The basal segment of the antenna is enlarged to form an eye cap; the maxillary palps are long; and the labial palps are short. The male has a well-developed frenulum, but the frenulum of the female consists of only a few small bristles. Most species in this group are leaf miners in trees or shrubs. The mines are linear when the larvae are young and are often broadened when the larvae become fully developed. The larvae usually leave the mines to pupate, spinning cocoons in debris on the surface of the soil. A few species in the genus *Ectoedemia* are gall makers. Most North American species are in the genus *Stigmella* (= *Nepticula*).

***Family* Opostegidae:** The Opostegidae are small moths with linear hind wings and with unbranched radius, media, and cubitus of the front wings. The first segment of the antenna forms a large eye cap. The larvae are miners. This is a small group and contains the single genus *Pseudopostega*, with nine species in North America.

SUPERFAMILY Incurvarioidea: In this superfamily, the female has an elongate, piercing ovipositor.

***Family* Heliozelidae—Shield Bearers:** The heliozelids are small moths with lanceolate wings. The hind wings have no discal cell (Figure 30–33F). The larvae of the resplendent shield bearer, *Coptodisca splendoriferella* (Clemens), are both leaf miners and casebearers. The larvae make a linear mine in apple, wild cherry, and related trees, and this mine is later widened. When full grown, the larva makes a case from the walls of its mine, lines it with silk, and attaches it to a limb or to the trunk of the tree. There are two generations a year, with the larvae of the second generation overwintering in the cases. The front wings of the adult are dark gray at the base, the outer portion bright yellow with brown and silver markings. Thirty-one species of heliozelids occur in North America.

***Family* Adelidae—Fairy Moths:** In these small, day-flying moths, the antennae of the males are very long, usually more than twice as long as the wings. The larvae are leaf miners when young and case makers when older. They feed on the foliage of trees and shrubs. There are 18 North American species. The eastern species usually encountered is *Adela caeruleella* Walker.

***Family* Prodoxidae:** The moths in this group are often white, and the folded part of the maxillary palps is about two thirds as long as the width of the head (Figure 30–29E, *mxp*). The best-known moths in this group are the yucca moths (*Tegeticula*), of which four species are known. The yucca is pollinated solely by these insects. The female moth collects pollen from the yucca flowers by means of long, curled, spinelike maxillary tentacles (palps) and then inserts her eggs into the ovary of another flower. After ovipositing, she thrusts the pollen she has collected onto the stigma of the flower in which the eggs have been laid. This action ensures fertilization and the development of the yucca seeds on which the larvae feed. The perpetuation of the yucca is assured, as more seeds are developed than are needed for the larvae. The bogus yucca moths of the genus *Prodoxus* lack the maxillary tentacles and cannot pollinate yuccas. Their larvae feed in the stems or fruits of these plants.

Family **Incurvariidae:** These small, dark-colored moths have the wing venation very little reduced and the wing surface aculeate. The females have a piercing ovipositor. The larvae of the maple leaf-cutter, *Paraclemensia acerifoliella* (Fitch), are leaf mining when young and become casebearers when older. The older larvae cut out two circular pieces of the leaf and put them together to form a case. When the larva moves about, it carries this case with it and looks somewhat turtlelike. The winter is passed as a pupa inside the case. The adult moth is a brilliant steel blue or bluish green with an orange head.

SUPERFAMILY **Tischerioidea:** In this group, the fore wing has a closed discal cell and unmodified antennal scape. Only one family is included.

Family **Tischeriidae:** The Tischeriidae are small moths in which the costal margin of the front wing is strongly arched and the apex is prolonged into a sharp point. The hind wings are long and narrow, with reduced venation (Figure 30–33E). The antennal scape is unmodified, and the maxillary palps are small or absent. The larvae of most species make blotch mines in the leaves of oak or apple trees and blackberry or raspberry bushes. The apple-leaf trumpet miner, *Tischeria malifoliella* Clemens, is a common species in the East and often does considerable damage: The larva makes a trumpet-shaped mine in the upper surface of the leaf, overwinters in the mine, and pupates in the spring. There are two or more generations a year. About 50 species of Tischeriidae occur in North America.

SUPERFAMILY **Tineoidea:** The main synapomorphy of this superfamily is the presence in females of a pair of slender, ventral pseudapophyses in A10. Additional characters are the presence of erect scales on the frons, the presence of lateral bristles on the labial palps, and the haustellum with short, dissociated galeae.

Family **Tineidae:** Most tineids (about 125 North American species) are small moths, in which the venation is rather generalized (or somewhat reduced), R_5 terminating on the costa. The maxillary palps have five segments and are usually large and folded, and the labial palps are short. The larvae of many species are casebearers. Some are scavengers or feed on fungi, and some feed on woolen fabrics. The species in this group that attack clothes and woolens (the clothes moths) are of considerable economic importance.

The most common clothes moth is the webbing clothes moth, *Tineola bisselliella* (Hummel). The adult is straw colored, without dark spots on the wings, and has a wingspread of 12–26 mm. The larvae feed on hair fiber, woolens, silks, felt, and similar materials. They do not form cases. When full grown, the larva forms a cocoon of fragments of its food material fastened together with silk.

Second in importance among the clothes moths is the case-making clothes moth, *Tinea pellionella* L. (Figure 30–36), which forms a case from silk and fragments of its food material. This case is tubular and open at each end. The larva feeds from within the case and pupates in it. The adult is brownish, with three dark spots on each front wing.

The clothes moth of the least importance in the United States is the carpet moth, *Trichophaga tapetzella* (L.), which builds rather long, silken tubes or galleries to go through certain fabrics, on which it may not feed. These tubes often have fragments of cloth woven in the silk. Where this species is found, it is quite destructive. The adult has a wingspread of 12–24 mm, and the front wings are black at the base and white in the apical portion.

Some authorities place the genera *Phaeoses, Opogona,* and *Oinophila* in the Hieroxestidae (= Oinophilidae), but Davis (1978b) places them in the Tineidae. They are small (wingspread 7.5 to 22.0 mm, mostly 15 mm or less) and usually rather plain-colored. They differ from most Tineidae in having a smooth-scaled head and differ from many other microlepidoptera in having well-developed maxillary palps (two-segmented and relatively short in *Phaeoses*, five-segmented and as long as the labial palps or longer in the other two genera). The moths occur in the southern states, from Florida to California. *Opogona sacchari* (Bojer), the banana moth, has recently become established in southern Florida. It is destructive to ornamental nursery plants such as cane (*Dracaena* spp.) and bamboo.

Family **Acrolophidae:** This group, the burrowing webworms, consists of small to medium-sized moths

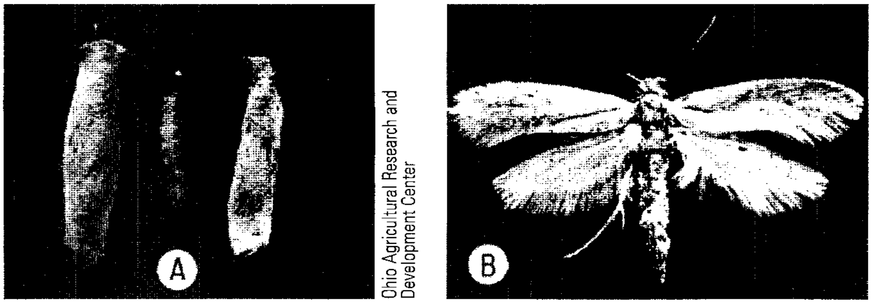

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Figure 30–36 The case-making clothes moth, *Tinea pellionella* (L.). A, larvae and cases; B, adult, 2½×.

that resemble noctuids. The first segment of the labial palps is as large as the second or larger (Figure 30–29D); the eyes are usually hairy; and the venation is complete, with three anal veins in both front and hind wings, and R_5 terminating on the termen (distal margin) or apex. The 48 North American species in this group are placed in the genus *Acrolophus*. The larvae make a tubular web in the ground, sometimes extending as deep as 0.6 m, into which they retreat when disturbed. They feed on the roots of grasses and also web the grass blades at the surface. These insects often destroy entire young corn plants.

Family **Psychidae—Bagworms**: These moths are so named because of the characteristic bags or cases that the larvae make and carry about. These bags are easily seen on trees during the winter after the leaves have fallen (Figure 30–37). The bags are made of silk and portions of leaves and twigs. The larvae pupate in the bags, and most species overwinter as eggs in the bags. When the larvae hatch in the spring, they construct their cases and carry them about as they feed. When full grown, they attach the case to a twig, close it, and pupate inside it.

The adult males of this group are generally small, with well-developed wings, but the females are wingless, legless, and wormlike and normally do not leave the bag in which they pupated. On emerging the males fly about and locate a bag containing a female. Mating takes place without the female leaving the bag, and the eggs are later laid in the bag.

Thyridopteryx ephemeraeformis (Haworth) is a common species of bagworm, the larvae of which attack chiefly red cedar and arborvitae. The adult males are small, dark-colored, heavy-bodied moths with large, clear areas in the wings.

SUPERFAMILY **Gracillarioidea:** Douglasiidae, Bucculatricidae, and Gracillariidae differ from Tineoidea and Yponomeutoidea by the pupa bearing abdominal tergal spines, adult males lacking pleural lobes on abdominal segment 8, frons smoothly scaled, and the labial palps without bristles.


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Figure 30–37 Bags of the bagworm, *Thyridopteryx ephemeraeformis* (Haworth).

Family **Douglasiidae:** The Douglasiidae are leaf miners in the larval stage, and the adults are small moths with lanceolate hind wings that lack a discal cell (Figure 30–33B). Rs in the hind wing separates from the media near the middle of the wing. The ocelli are large. Only seven species of douglasiids occur in North America. The larvae of *Tinagma obscurofasciella* (Chambers) mine in the leaves of plants in the family Rosaceae.

Family **Bucculatricidae:** These small moths have very narrow wings. The hind wings are often linear, with Rs extending through the center of the wing (Figure 30–33A). Ocelli and maxillary palps are usually lacking. The frons projects below the eye, the vertex usually has an erect tuft of scales, the antennal scape is enlarged and has a row of scales that partially covers the eye, and the haustellum is short (1.5× diameter of eye or less). The larvae are leaf miners or live in webs between the leaves. The apple bucculatrix, *Bucculatrix pomifoliella* Clemens, overwinters in rows of white, longitudinally ribbed cocoons on the twigs of apple. The adults emerge in the spring and oviposit on the lower surface of the leaves. The larvae enter the leaf and make a serpentine mine on the upper surface. Silken molting cocoons are made on the surface of the leaf before the pupal cocoons are formed. Approximately 100 species of *Bucculatrix* occur in North America.

Family **Gracillariidae—Leaf Blotch Miners**: This is a large group (275 North American species) of small to minute moths with lanceolate wings. The front wing usually lacks an accessory cell, and the cilia of the hind wing are longer (often much longer) than the width of the wing; and in some species there is a hump along the costal margin near the base (Figure 30–33D). The adult moths at rest elevate the anterior part of the body, with the wing tips touching the surface on which the moth rests. The larvae usually make blotch mines, and the leaf is often folded.

The white-oak leaf miner, *Cameraria hamadryadella* (Clemens), is a common eastern species that feeds on various types of oak. The mines are on the upper surface of the leaves, and each mine contains a single larva. Many mines may occur on a single leaf (Figure 30–38A). The larvae are flattened, with only rudiments of legs and with an enlarged prothorax. The larva pupates in a delicate cocoon inside the mine. It overwinters as a larva in dry leaves. The adult moth is white with broad, irregular, bronze bands on the front wings.

Some species of *Phyllocnistis* make winding serpentine mines in aspen leaves (Figure 30–38B). The larva usually starts near the tip of the leaf and mines toward the base, and it often must go out toward the edge of the leaf to get across a large vein. It pupates in

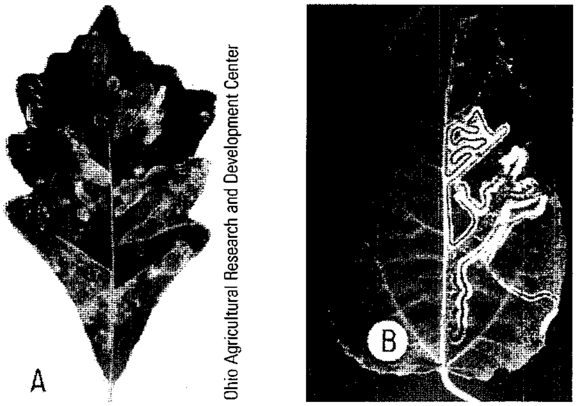

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Figure 30–38 Leaf mines of Gracillariidae. A, the whiteoak leafminer, *Cameraria hamadryadella* Clemens; B, an aspen leafminer, *Phyllocnistis* sp.

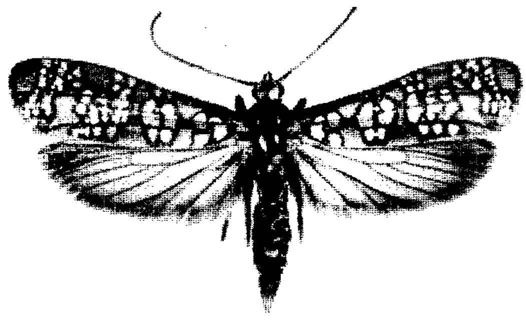

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Figure 30–39 An ermine moth, *Atteva* sp. (Yponomeutidae), $2\frac{1}{2}\times$.

a silken cocoon at the end of the mine, usually at the basal edge of the leaf.

SUPERFAMILY Yponomeutoidea: This somewhat heterogeneous group of families is characterized by males having posterior expansions of pleuron 8 that enclose the genitalia. These moths have a naked haustellum, which separates them from similar-appearing Gelechioidea.

***Family* Yponomeutidae—Ermine Moths:** The Yponomeutidae are small and usually brightly patterned moths with rather narrow wings (Figure 30–39). The branches of the main veins in the front wing are generally separate, and R_5 extends to the outer margin of the wing. Rs and M_1 in the hind wing are separate (Figure 30–32). The ocelli are absent. The moths in the genus *Yponomeuta* have front wings that are white dotted with black. Their larvae feed on rosaceous plants, such as cherry and apple. The larvae of the ailanthus webworm, *Atteva punctella* (Cramer), live in a frail silken web on the leaves of ailanthus and feed on the leaves. The pupae are suspended in loose webs. The front wings of the adult are bright orange, marked with four transverse bands of lead blue, each enclosing a row of yellow spots (Figure 30–39). There are several forms of this species, with varying amounts of yellow spotting. The pine needle sheath miner, *Zelleria haimbachi* Busck, is widely distributed and attacks various pines, sometimes doing quite a bit of damage. The first-instar larvae mine in needles, and later instars feed in the sheath at the base of the needle cluster, severing the needles and causing them to be shed. Each larva kills 6 to 10 needle clusters.

The moths in the subfamily Argyresthiinae have narrower wings (hind wings lanceolate, with reduced venation), and the fused bases of M_1 and M_2 in the hind wing form a long stalk. The Plutellidae have similar venation, but have ocelli (lacking in the Argyresthiinae). The larvae of these moths bore in twigs, buds, and fruits or are leaf miners, generally attacking various trees.

The genus *Argyresthia* contains about 50 species whose members attack the leaves, buds, and twigs of various trees. The arborvitae leaf miner, *A. thuiella* (Packard), attacks the leaves of cedar. The adults are white moths with the fronts wings spotted with brown and have a wingspread of about 8 mm. Many members of this group have metallic markings in the front wings. The adults often rest with the head against the substrate and the body held up on an angle.

***Family* Ypsolophidae:** Moths in this family have Rs and M_1 stalked or coincident in the hind wing, the ocelli are present, and the head is rough scaled. *Ypsolopha* with 33 species and the single species of *Ochsenheimeria* constitute the family in North America. Larvae of *Ypsolopha* make open webs on many (mainly woody) plants. *Ochsenheimeria* is an Old World genus, one species of which has apparently become established in the Northeast. This species is the cereal stem moth, *Ochsenheimeria vacculella* F. von Roeslerstamm, which is a pest of winter wheat and rye in Europe and may become a similar pest in the United States. These are small (wingspread 11–14 mm), slender-bodied moths, with the front wings a mottled brownish and the hind wings pale. They can be recognized by the characters in the key (couplet 78).

These moths oviposit in late summer on straw piles in the fields, and the eggs hatch in the spring. The young larvae mine in the leaf blades, and older larvae burrow into the stems. Pupation occurs between the leaves of the host plant, and the moths emerge in early June.

Family **Plutellidae—Diamondback Moths:** The Plutellidae are similar to the Yponomeutidae, but they hold their antennae forward at rest, and M$_1$ and M$_2$ in the hind wings are stalked. They differ from the Ypsolophidae in having Rs and M$_1$ separate in the hind wing, and from Acrolepiidae in having M$_2$ and CuA$_1$ separate in the hind wing. The name "diamondback" refers to the fact that in the males of *Plutella xylostella* (L.) the wings, when folded, show a series of three yellow, diamond-shaped marks along the line where the wings meet. This species is a major pest of cabbage and other cruciferous plants. The larvae eat holes in the leaves and pupate in silken cocoons attached to the leaves. There are 20 species of plutellids in North America.

Family **Acrolepiidae:** These small moths are similar to the Plutellidae but have the maxillary palps of the folded type (porrect in the Plutellidae) and smooth labial palps (with a tuft in the Plutellidae). This group is a small one, with only three North American species. One of these, *Acrolepiopsis incertella* (Chambers), occurs in the northern part of the United States, from New England to California. Its larva skeletonizes the leaves of *Smilax* or possibly bores in the stems of lilies. The adult's wings are gray brown, with reddish iridescence and an oblique white stripe extending from the inner margin near the base to about the middle of the wing.

Family **Glyphipterigidae:** The members of this group are small diurnal moths, 7–15 mm in length, with relatively large ocelli and with the wings shaped much like those in Figure 30–30B. The larvae feed mostly as seed borers in sedges and rushes. The most common North American species, *Glyphipterix impigritella* (Clemens), is found in the East, and also in the West from British Columbia to California and Nevada. Its larva is a stem and leaf axil borer of *Cyperus*. Thirty-six species of glyphipterigids occur in North America.

Family **Heliodinidae:** The heliodinids are small diurnal moths with hind wings that are very narrow and lanceolate and have a broad fringe; the fore wing has only five veins arising from the cell behind the apex. The entire head is smoothly scaled, the ocelli are present, and the proboscis is naked. The adult at rest usually holds the hind legs elevated above the wings. The family is a small one (20 North American species), and the known larvae vary in habits. The larvae of *Cycloplasis panicifoliella* Clemens mine in the leaves of panic grass, forming at first a linear mine that is later enlarged to a blotch. Members of the genus *Heliodines* are brightly colored orange and black day-flying moths that feed on *Mirabilis* (four o'clock) in the midwest.

Family **Bedelliidae:** The single genus *Bedellia*, with two North American species, lacks ocelli, has narrow wings (Figure 30–33A), and has R$_{3-5}$ and M stalked in the fore wing. The leaf-mining larva of *Bedellia somnulentella* (Zeller) may be a pest of *Ipomoea*.

Family **Lyonetiidae:** Adults are very similar to those of Bedelliidae, but the antennal scape is expanded into an eye cap. The larvae are leaf or twig miners. Pupation occurs outside the mine. About 20 species of lyonetiids occur in North America.

SUPERFAMILY **Gelechioidea:** Moths of this large superfamily have a scaled base of the proboscis, upturned labial palps, the maxillary palps scaled and folded over the base of the proboscis, and the head smoothly scaled; they lack thoracic or abdominal tympana, and chaetosemata. Recent study has produced a new classification based on characters of the immature and adult stages (Hodges, in Kristensen, 1998).

Family **Elachistidae:** Species of Elachistidae have lateral condyles between abdominal segments 5 and 6 and 6 and 7 of the pupa. The five subfamilies, with 331 species, occur widely in North America.

Subfamily Stenomatinae: These moths are larger than most microlepidoptera, and the wings (Figure 30–31D) are relatively broad (Figure 30–40D). The larvae live in webs on the leaves of oaks and other trees. *Antaeotricha schlaegeri* (Zeller) is a fairly common eastern species. The adult has a wingspread of about 30 mm, and the wings are grayish white with dark markings. When at rest, this moth resembles bird excrement. Most species are Neotropical.

Subfamily Ethmiinae: A few species in this group are plain colored, but most are rather brightly patterned, often black and white. Their larvae feed principally on the leaves and flowers of plants in the borage and waterleaf families (Boraginaceae and Hydrophyllaceae). *Ethmia discostrigella* (Chambers) is a defoliator of mountain mahogany (*Cercocarpus*). Outbreaks of this insect deplete the winter ranges of big game in Oregon and other western areas. Most of the 50 North American species of Ethmiinae occur in the West.

Subfamily Depressariinae: These are small and somewhat flattened moths, with the wings relatively broad and rounded apically (Figure 30–40B). The venation (Figure 30–32A) is complete, with CuP preserved in the front wing, R$_4$ and R$_5$ in the front wing stalked or coalesced throughout their entire length, and Rs and M$_1$ in the hind wing separate and parallel. The parsnip webworm, *Depressaria pastinacella* (Duponchel), attacks parsnip and related plants. The larvae web together and feed on the unfolding blossom heads, and then burrow into the stems to pupate. The adults appear in late summer and hibernate in protected situations.

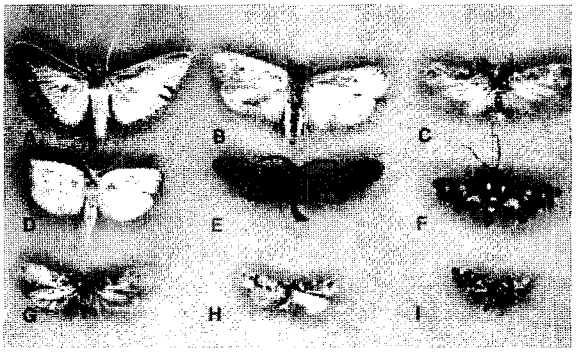

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Figure 30–40 Miscellaneous microlepidoptera. A, *Diaphania hyalinata* L. (Crambidae, Pyraustinae; adult of the melonworm); B, *Depressaria pastinacella* (Duponchel) (Elachistidae, Depressariinae; adult of the parsnip webworm); C, *Gnorimoschema gallaesolidaginis* (Riley) (Gelechiidae; a goldenrod gall moth); D, *Stenoma algidella* Walker (Elachistidae, Stenomatinae); E, *Harrisina americana* (Guérin) (Zygaenidae; adult of the grape leaf skeletonizer); F, *Thyris lugubris* Boisduval (Thyrididae); G, *Blastobasis glandulella* (Riley) (Coleophoridae, Blastobasinae; the acorn moth); H, *Fascista cercerisella* (Chambers) (Gelechiidae); I, *Stagmatophora sexnotella* (Chamber) (Cosmopterigidae).

Subfamily Elachistinae—Grass Miners: The adults of this group have lanceolate hind wings that have a well-formed discal cell. The venation is only slightly reduced (Figure 30–34A). This subfamily has 155 North American species.

Subfamily Agonoxeninae: This is a small but widely distributed group, many of whose members have previously been placed in other families. Little is known of their larval habits, but larvae of *Chrysochista linneella* (Clerck) feed in the cambium of *Tilia*, and some *Blastodacna* are nut and fruit borers.

Subfamily Chimabachinae: This is primarily a European group, and only one species, *Cheimophila salicella* (Hübner), occurs in North America. It was introduced into British Columbia, where it is a pest on high-bush blueberry. This group is considered to be an independent family in some classifications. The larvae have the metathoracic tibiae and tarsi swollen.

***Family* Xyloryctidae:** The subfamily Scythridinae of this family occurs in North America. According to Landry (1991), these 41 species known may be less than 10% of the true extent of the family's diversity. Superficial similarity belies extreme structural diversity in genital characters. Adult moths usually can be recognized by the extremely smoothly scaled head and labial palps, ocellus (when present) slightly separated from the eye, and R_4 and R_5 stalked in the fore wing with R_4 to anterior margin and R_5 to termen. Moths are diurnal or nocturnal. The larvae of *Scythris magnatella* Busck feed on willow herbs (*Epilobium*), folding over a portion of the leaf for an individual cell.

***Family* Glyphidoceridae:** *Glyphidocera*, with 10 species, is the only genus of this mainly Neotropical family in North America. Larvae of *Glyphidocera juniperella* Adamski feed on *Juniperus*.

***Family* Oecophoridae:** These moths are often very colorful. *Hofmannophila pseudospretella* (Stainton) is a minor household pest, originally from Europe. The larvae feed mainly on dead plant tissue, possibly on fungi.

***Family* Batrachedridae:** Adults have slender wings with a wide fringe on the hind wing. Most of the 24 species belong to the genus *Batrachedra*. This family includes the palm leaf skeletonizer, *Homaledra sabalella* (Chambers), which occurs in the southern states, where its larvae feed on the upper surface of the leaves of the saw palmetto. A group of larvae make a delicate silken cover over the injured portion of the leaf and cover it with their droppings.

***Family* Deoclonidae:** This very small family has one species in North America, *Deoclona yuccasella* Busck, reared the larva from old pods of *Yucca whipplei*.

***Family* Coleophoridae:** Three of the four subfamilies have a large number of species. Although abundant, they are infrequently collected.

Subfamily Coleophorinae—Casebearers: The moths in this subfamily are small, with very narrow, sharply pointed wings. The discal cell in the front wing is oblique, and veins Cu_1 and Cu_2 (when present) are very short. There are no ocelli or maxillary palps. About 150 species, most in the genus *Coleophora*, occur in the United States. The larvae are usually leaf miners when young and casebearers when they become larger.

The pistol casebearer, *Coleophora malivorella* Riley, is a common pest of apple and other fruit trees. The larvae construct pistol-shaped cases of silk, bits of leaves, and excrement, which they carry about. By protruding their heads from these cases, they eat holes in the leaves. They overwinter as larvae in the cases, and the moths appear in midsummer.

The cigar casebearer, *Coleophora serratella* (L.), also attacks apple and other fruit trees (Figure 30–41). This species is similar to the preceding casebearer except that the young larvae are miners in the leaves for two or three weeks before making their cases.

Subfamily Blastobasinae: The Blastobasinae are small moths in which the hind wings are somewhat lanceolate and narrower than the front wings (Figure 30–30B). The membrane of the front wing is slightly thickened along the costa. The larva of the acorn moth, *Blastobasis glandulella* (Riley) (Figure 30–40G), feeds inside acorns that

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Figure 30–41 Larvae (in their cases) of the cigar casebearer, *Coleophora serratella* (L.), on an apple leaf.

have been hollowed out by the larvae of acorn weevils. The larvae overwinter in the acorns, and the adults appear the following summer. Species of *Holcocera* attack conifers in the West. The larvae of *Zenodochium coccivorella* (Chambers) are internal parasites of female gall-like coccids of the genus *Kermes*. This species has been found in Florida. There are 113 North American species of blastobasines.

Subfamily Momphinae: These moths are small, with the wings long and narrow and usually sharply pointed at the apex. They are very similar to some Elachistinae, and Cosmopteriginae, and because these families are separated principally by the structure of the male genitalia, some genera in these families cannot be separated by our key (which is based principally on wing venation). Most momphines have subtle but colorful fore wing patterns, especially at the apex of the wing. Most of the 40 North American species are in the genus *Mompha*. Their larvae mainly mine or form galls on members of the Onagraceae.

***Family* Autostichidae:** The three genera and species are infrequently collected. Their larvae are scavengers on plant tissue. Most species occur in dry areas of the Palearctic from the Mediterranean to China.

***Family* Peleopodidae:** This tropical group occurs in the United States only in the extreme South. Two species occur in North America.

***Family* Amphisbatidae:** Species of this family were included in Oecophoridae. Genital and abdominal characters serve for recognition of this mainly New World group. The larvae of *Machimia tentoriferella* Clemens roll or tie leaves of species in nearly 20 plant genera. Adults of *Psilocorsis reflexella* Clemens are highly variable in color pattern and genital characters.

***Family* Cosmopterigidae:** This is a fair-sized group (180 North American species) of small moths that have long, narrow wings, usually sharply pointed at the apex (Figure 30–42B). Some species are rather brightly colored. Most of these moths are leaf miners in the larval stage. The larvae of the cattail moth, *Lymnaecia phragmitella* Stainton, feed in cattail heads. The pink scavenger caterpillar, *Pyroderces rileyi* (Walsingham) (Figure 30–42B), feeds in cotton bolls. A somewhat aberrant member of this group, *Euclemensia bassettella* Clemens (placed in the subfamily Antequerinae), is an internal parasite of female gall-like coccids of the genus *Kermes*. Most species of the genus *Cosmopterix*, which look similar the world over, are dark-colored with a golden band near the apex of each front wing.

***Family* Gelechiidae:** This family is one of the largest of the microlepidoptera (about 850 North American

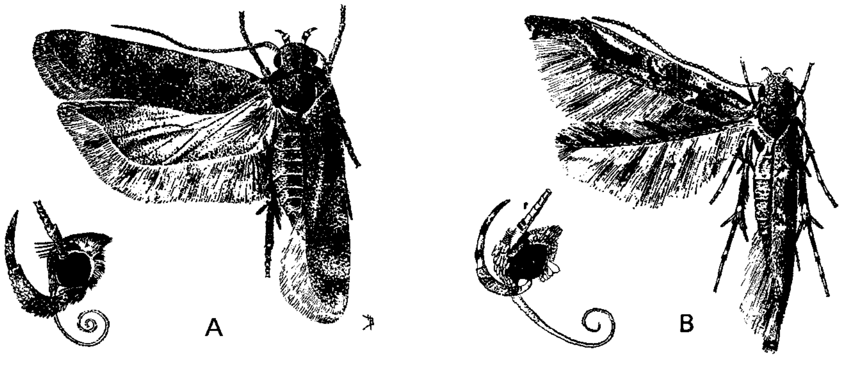

Figure 30–42 A, the pink bollworm, *Pectinophora gossypiella* (Saunders) (Gelechiidae); B, adult of the pink scavenger caterpillar, *Pyroderces rileyi* (Walsingham) (Cosmopterigidae); 4×. Inserts: lateral views of heads. (Courtesy of Busck and the USDA Journal of Agricultural Research.)

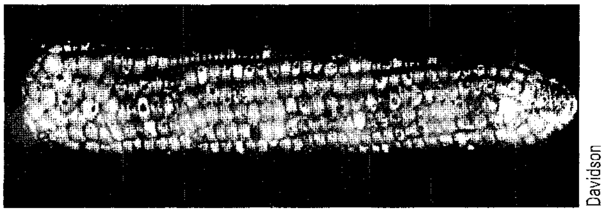

Figure 30–43 Injury to corn by the Angoumois grain moth.

species), and many species are fairly common. The moths are all rather small (Figure 30–40C,H). Veins R_4 and R_5 in the front wing are stalked at the base (rarely, they are fused for their entire length), and A_{1+2} is forked at the base. The hind wing usually has the outer margin somewhat pointed and recurved (Figure 30–31C). Gelechiid larvae vary in habits. Some are leaf miners; a few form galls; many roll or tie leaves; and one species is a serious pest of stored grain.

The Angoumois grain moth, *Sitotroga cerealella* (Olivier), is an important pest of stored grain. The larva feeds in the kernels of corn, wheat, and other grains, and the emerging adult leaves a conspicuous emergence hole at one end of the kernel (Figure 30–43). The grain may become infested with this insect either in the milk stage of the growing grain or in storage. Stored grain may be completely destroyed by it. The adult moth is light grayish brown with a wingspread of about 13 mm.

The pink bollworm, *Pectinophora gossypiella* (Saunders) (Figure 30–42A), is a serious pest of cotton in the South and Southwest. The larvae attack the bolls, and losses of up to 50% of the crop are not uncommon in fields that are infested with this insect.

Many species in the genus *Gnorimoschema* form galls in the stems of goldenrod, different species attacking different species of goldenrod. The galls are elongate, spindle-shaped, and rather thin-walled (Figure 30–44). The larva pupates in the gall, but before pupating it cuts an opening (not quite completely through the wall) at the upper end of the gall. When the adult emerges, it can easily push out through this opening. Pupation occurs in middle or late summer, and the adults (Figure 30–40C) emerge and lay their eggs on old goldenrod plants in the fall. The eggs hatch the following spring.

Phthorimaea operculella (Zeller), the potato tuberworm, is a pest of potatoes and related plants. The larvae mine in the leaves and bore into the tubers. *Aroga websteri* Clarke periodically defoliates and kills sagebrush over large areas of western range land. Species in the genus *Coleotechnites* are leaf miners in conifers. A few are sometimes serious pests.

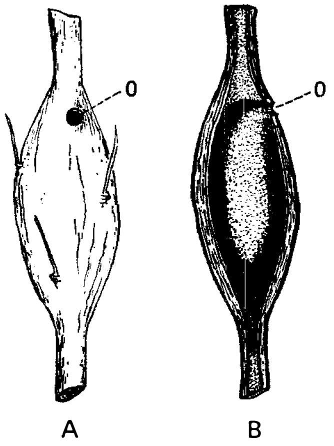

Figure 30–44 Gall of the goldenrod gall moth, *Gnorimoschema* sp. (Gelechiidae). A, exterior view; B, a gall cut open. *o*, opening; cut by the larva before pupating, through which the emerging adult escapes.

SUPERFAMILY Zygaenoidea: Six families make up the Zygaenoidea in North America. They are associated by the late-instar larva having a retractable head. Most are infrequently collected.

***Family* Epipyropidae—Planthopper Parasites:** These moths are unique in that the larvae are parasites of planthoppers (Fulgoroidea) and other Hemiptera Auchenorrhyncha. The moth larva feeds on the dorsal surface of the abdomen of the planthopper, under the wings. These moths are relatively rare, and only a single species occurs in the United States. This is *Fulgoroecia exigua* (Edwards), a dark brownish-purple moth with broad wings, pectinate antennae, and a wingspread of 8–13 mm.

***Family* Megalopygidae—Flannel Moths:** These moths have a dense coat of scales mixed with fine, curly hairs, which give the insects a somewhat woolly appearance. They are medium-sized to small and usually brownish in color. The larvae are also hairy, and in addition to the usual five pairs of prolegs, they have two pairs that are suckerlike and lack crochets. The larvae have stinging spines under the hairs and can cause even more irritation than the saddleback caterpillars. The cocoons are tough and are provided with a lid as in the Limacodidae. They are usually formed on twigs. The crinkled flannel moth, *Lagoa crispata* (Packard), is a common eastern species. It is a yellowish moth with brownish spots or bands on the wings and has a wingspread of a little over 25 mm. The larva feeds on blackberry, raspberry, apple, and other plants. This group is a small one, with only 11 North American species.

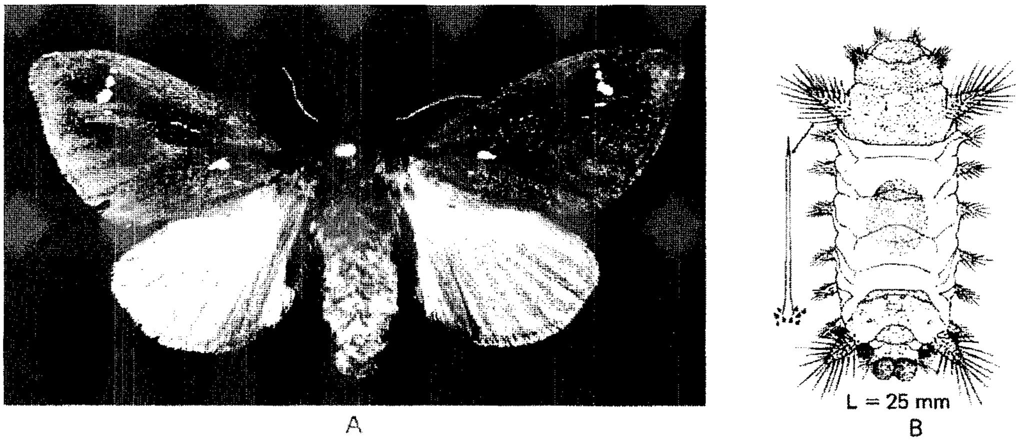

Figure 30–45 Adult (A) and larva (B) of the saddleback caterpillar, *Sibine stimulea* (Clemens). A, 3×. (A, courtesy of Dwight M. DeLong; B, courtesy of Peterson. Reprinted by permission.)

Family **Limacodidae—Slug Caterpillars:** These insects are called "slug caterpillars" because the larvae are short, fleshy, and sluglike. The thoracic legs are small, there are no prolegs, and the larvae move with a creeping motion. Many of the larvae are curiously shaped or conspicuously marked. The cocoons are dense, brownish, and oval and have a lid at one end that is pushed out by the emerging adult. The adult moths (Figure 30–45A) are small to medium-sized, robust, and hairy and are usually brownish and marked with a large, irregular spot of green, silver, or some other color.

One of the most common species in this group is the saddleback caterpillar, *Sibine stimulea* (Clemens). The larva (Figure 30–45B) is green with a saddlelike brown mark on the back. These larvae have stinging hairs and can cause severe irritation to the skin. They feed principally on various trees.

Family **Dalceridae:** This is a Neotropical group, one species of which has been reported from Arizona: *Dalcerides ingenita* (Edwards). This moth is rather woolly and resembles a flannel moth. It has dark yellow or orange front wings, orange hind wings, and a wingspread of 18–24 mm.

Family **Lacturidae:** The six species of *Lactura* were formerly placed in Yponomeutidae. They are mainly southern. *Lactura pupula* (Hübner) of the Southeast has cream-colored fore wings that have black lines anteriorly and distally and black spots posteriorly. The hind wings are uniformly orange.

Family **Zygaenidae—Smoky Moths and Burnets:** The smoky moths are small, gray or black moths, usually with a reddish prothorax and often with other bright markings. Some exotic species, such as the European burnets and some large Chinese species, are often very colorful. The larvae have tufted hairs, and the more common North American species feed on grape or Virginia creeper. The grape leaf skeletonizer, *Harrisina americana* (Guérin-Méneville), is a common species in this group. The adult is a small, narrow-winged, smoky moth with a reddish collar (Figure 30–40E), and the larvae are yellow with black spots. A number of these larvae feed on the same leaf, lined up in a row and backing up as they skeletonize the leaf. There are 22 North American species of smoky moths.

SUPERFAMILY Sesioidea: The Sesiidae is the only family of Sesioidea in America north of Mexico.

Family **Sesiidae—Clearwing Moths:** The greater part of one or both pairs of wings in this family lacks scales, and many species very strikingly resemble wasps (Figure 30–46). The front wings are long and narrow, with the anal veins reduced, and the hind wings are broad, with the anal area well developed (Figure 30–47). The sesiids have a wing-coupling mechanism somewhat similar to that in the Hymenoptera. Many species are brightly colored, and virtually all are active during the day. The two sexes are often colored differently, and in some cases they differ in the amount of clear area in the wings. The larvae bore in the roots, stems, canes, or trunks of plants or trees and often cause considerable damage. There are 115 species of sesiids in North America.

The peach tree borer, *Synanthedon exitiosa* (Say), is one of the most important species in this family. The females lay their eggs on the trunks of peach trees near the ground, and the larvae bore into the tree just below the surface of the ground, often girdling the tree. There is one generation a year, and the larvae overwinter in

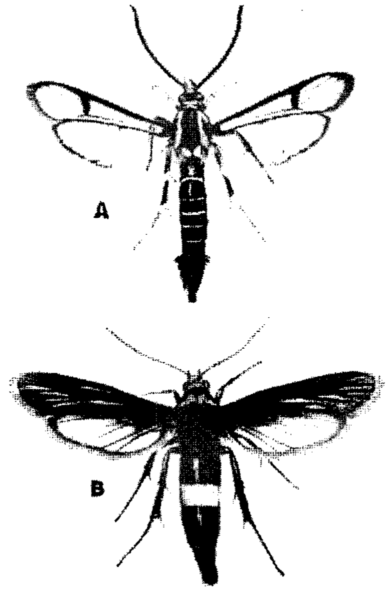

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Figure 30–46 The peach tree borer, *Synanthedon exitiosa* (Say) (Sesiidae), 1½×. A, male; B, female.

their burrows in the tree. The female has the front wings fully scaled, and the abdomen is marked with a broad orange band. The male has both the front and the hind wings largely clear, and the abdomen is ringed with several narrow yellow bands (Figure 30–46). The adults are active throughout the summer. The lesser peach tree borer, *S. pictipes* (Grote and Robinson), has similar habits, but the larvae generally bore into the trunk and larger branches. Both sexes resemble the male of *S. exitiosa*.

The squash vine borer, *Melittia cucurbitae* (Harris), is a serious pest of squash and related plants. The larvae bore into the stems and often destroy the plant. This species overwinters as a pupa in the soil. The adults are a little larger than those of the peach tree borer and have olive green front wings and clear hind wings. The hind legs are heavily clubbed, with a long fringe of orange scales.

The currant borer, *Synanthedon tipuliformis* (Clerck), is a small moth with a wingspread of about 18 mm. The larva bores in the stems of currants, and pupation occurs in the stems. The adults appear in early summer.

Sesiid sex pheromones have been synthesized for the capture of the males of such pest species as the peach tree borer, and these pheromones attract almost all male sesiids.

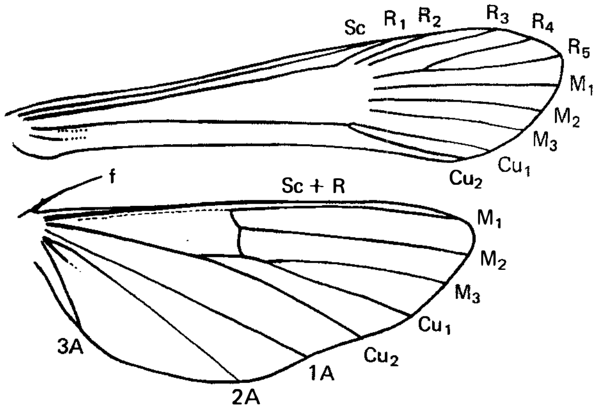

Figure 30–47 Wings of *Synanthedon* (Sesiidae). *f*, frenulum.

Family **Cossidae—Carpenter Moths and Leopard Moths:** The cossids bore and feed in wood in the larval stage, and this habit defines the family within the higher Lepidoptera. The adults are medium-sized and heavy-bodied, and the wings are usually spotted or mottled. The carpenterworm, *Prionoxystus robiniae* (Peck), is a common species that attacks various trees. The adult (Figure 30–48A) is a mottled gray and has a wingspread of about 50 mm. These insects may sometimes seriously damage trees. The leopard moth, *Zeuzera pyrina* (L.), a slightly smaller moth with the wings pale and marked with large black dots (Figure 30–48B), has similar habits. These moths require two or three years to complete their life cycle. About 45 species occur in North America.

SUPERFAMILY Tortricoidea: All females in members of the single family Tortricidae have large, flattened ovipositor lobes. Vein CuA_2 arising well before the end of the fore wing cell is characteristic of adults.

Family **Tortricidae:** This is one of the largest families of the microlepidoptera, with about 1,200 North American species, and many of its members are common moths. This group contains a number of important pest species. These moths are small, usually gray, tan, or brown, and often have dark bands or mottled areas in the wings, or occasionally colorful with metallic spots. The front wings are usually rather square-tipped. The wings at rest are held rooflike over the body. The larvae vary in habits, but many species roll or tie leaves, usually feeding on perennial plants. Many bore into various parts of the plant.

A tortricid that is an important pest of apples and other fruits is the codling moth, *Cydia pomonella* (L.) (Figure 30–49). The adults appear in late spring and lay their eggs, which are flattened and transparent, on

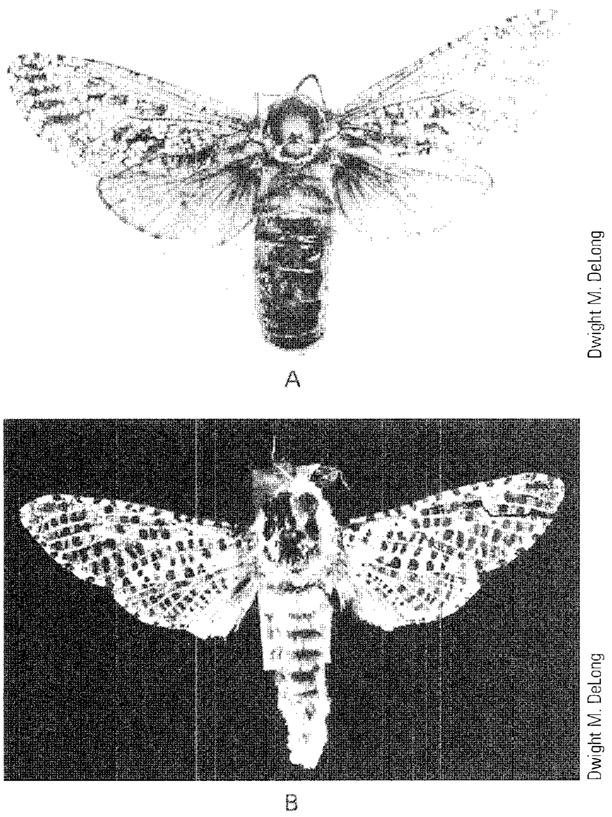

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Figure 30–48 Cossid moths. A, the carpenter moth, *Prionoxystus robiniae* (Peck), 1½×; B, the leopard moth, *Zeuzera pyrina* (L.), 1½×.

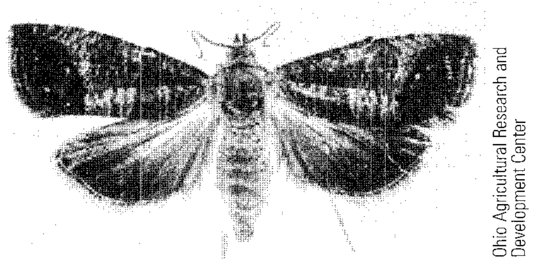

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Figure 30–49 The codling moth, *Cydia pomonella* (L.), 3×.

the surface of leaves. The young larvae crawl to young apples and chew their way into the fruits, usually entering by the blossom end. They are light-colored with a dark head. They complete their development in the fruits and pupate in the ground, under bark, or in similar situations. In the eastern United States a second generation follows in the late summer, with the full-grown larvae overwintering in cocoons under the bark of apple trees and in other protected places.

The oriental fruit moth, *Grapholitha molesta* (Busck), is an oriental species that is widely distributed in the United States. It is a serious pest of peaches and other fruits. It has several generations a year. The larvae of the first generation bore into the young green twigs, and the later-generation larvae bore into the fruits much as the codling moth does. The winter is passed as a full-grown larva in a cocoon.

This group includes a number of important forest pests. Perhaps the most serious are the spruce budworms: *Choristoneura*, particularly *C. fumiferana* (Clemens) in the East and *C. occidentalis* Freeman in the West (Figure 30–50). These insects are very serious defoliators, feeding on the buds of new foliage, and they sometimes explode in large outbreaks. Sustained attacks will kill a tree. The western black-headed budworm, *Acleris gloverana* (Walsingham), often causes extensive damage to various conifers in the West Coast states and in western Canada. It also sometimes occurs in outbreak numbers. The genus *Rhyacionia* contains the pine tip moths—several species whose larvae mine in the buds and shoots of young pines. The attacked

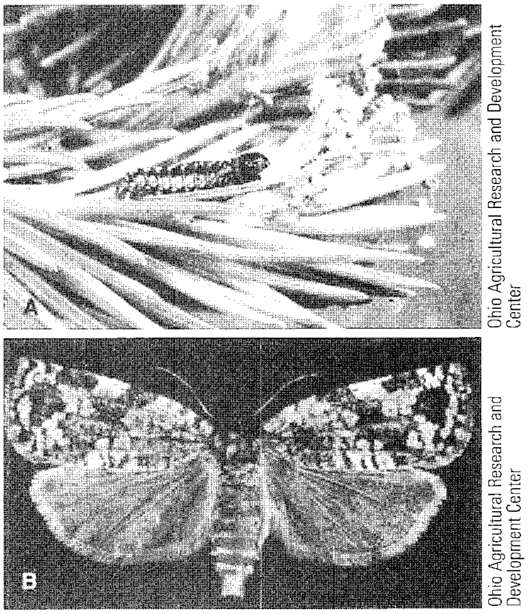

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Figure 30–50 Larva (A) and adult (B) of the spruce budworm, *Choristoneura fumiferana* (Clemens).

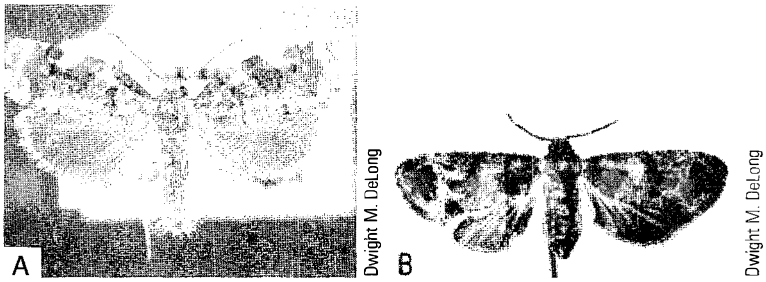

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Figure 30–51 A, adult of the fruit tree leafroller, *Archips argyrospilus* (Walker), 2× (Tortricidae); B, adult of the grape berry moth, *Endopiza viteana* Clemens, 4× (Tortricidae).

trees are seldom killed, but they are deformed and their growth is retarded. The fruit-tree leaf roller, *Archips argyrospilus* (Walker) (Figure 30–51A), is a rather common tortricid that makes an unsightly leaf nest in fruit and forest trees and often causes serious defoliation.

A number of other species in this family are occasionally destructive to various crops. The grape berry moth, *Endopiza viteana* Clemens (Figure 30–51B), feeds in the larval stage in the berries of grape. It has two generations a year. The strawberry leaf roller, *Ancylis comptana* (Frölich), attacks the foliage of strawberries and often does severe damage. The black-headed fireworm, *Rhopobota naevana* (Hübner), is a common pest that feeds on clover heads, destroying unopened buds and decidedly reducing the crop of seed. This insect has three generations a year and passes the winter as a pupa.

A species in this family that is something of a curiosity is the Mexican jumping-bean moth, *Cydia deshaisiana* (Lucas). The larva lives in the thin-walled seeds of *Sebastiana* and, after consuming the inside of the seed, throws itself forcibly against the thin wall when disturbed, causing the jumping movements of the seed.

This family is divided into three subfamilies, the Chlidanotinae, Tortricinae, and Olethreutinae.

The tribe Cochylini (Tortricinae) includes a number of species whose larvae are web-spinners and borers. Most attack herbaceous plants. The adults are similar to other Tortricidae, but vein CuP is completely lacking in the front wing, and Cu_2 in the front wing arises in the apical fourth of the discal cell; M_1 in the hind wing is usually stalked with Rs. *Aethes rutilana* (Hübner) attacks juniper, tying the leaves together to form a tube in which the larva lives. The adult of this species has a wingspread of about 25 mm, and the front wings are orange, marked with four brownish cross bands.

There are 110 North American species of Cochylini, and only three of the Chlidanotinae. The latter group is primarily tropical, and the North American species are in the genus *Thaumatographa* (= *Hilarographa*).

SUPERFAMILY Galacticoidea: The somewhat anomalous small family Galacticidae has one introduced species in North America.

***Family* Galacticidae:** This family includes the introduced mimosa webworm, *Homadaula anisocentra* Meyrick, which is a serious defoliator of mimosa and honey locust. This insect was first recorded in the United States in 1942, in Washington, DC. Since then it has spread southward to Florida and westward to Kansas and Nebraska, and there is a small colony in the vicinity of Sacramento, California.

SUPERFAMILY Choreutoidea: The single family Choreutidae has been placed in the Yponomeutoidea, but the scaled proboscis and very small maxillary palps are distinctive.

***Family* Choreutidae:** Members of this family are small diurnal moths, somewhat similar to the Tortricidae in general appearance but usually more colorful, with relatively broad wings, a scaled proboscis, and large ocelli. The larvae are mostly leaf tiers. The apple and thorn skeletonizer, *Choreutes pariana* (Clerck), is a pest of apple trees, especially in British Columbia. It ranges across southern Canada, going south into New England, Colorado, and Oregon. This species also occurs in Europe, from where it was introduced into North America. Tropical species sometimes come into Florida, and the total North American fauna of choreutids is about 40 species.

SUPERFAMILY Urodoidea: The mainly tropical family Urodidae is the only member of superfamily Urodoidea in North America.

***Family* Urodidae:** *Urodes parvula* (Hy. Edwards) occurs in Florida, where it may be common. The larva feeds on *Persea, Bumelia, Hibiscus,* and other plants. The European *Wockia asperipuntella* (Bruand) is an introduction to the Northeast.

SUPERFAMILY Schreckensteinioidea: Members of the single family are similar to heliodinids and stathmopodines in wing shape and the adult habit of holding the hind legs upward when at rest. They differ in lacking a scaled proboscis and ocelli.

Family **Schreckensteiniidae**: Three species of this family occur in North America. Larvae feed on sumac and *Rubus*.

SUPERFAMILY Epermenioidea: This superfamily has a single cosmopolitan family.

Family **Epermeniidae:** This is a small group (11 North American species) of moths formerly placed in the Scythrididae. The posterior margin of the fore wing usually has one or more triangular groups of scales. The larvae of *Epermenia pimpinella* Murtfeldt form puffy mines in parsley. The pupa is enclosed in a rather frail cocoon on the underside of a leaf or in an angle of a leaf stalk.

SUPERFAMILY Alucitoidea: Superfamily Alucitoidea, a small, worldwide group has one family in North America.

Family **Alucitidae—Many-Plume Moths**: The alucitids resemble the pterophorids, but have the wings split into six plumelike divisions. Only one named species in this family, *Alucita hexadactyla* L., occurs in the United States. The adults have a wingspread of about 13 mm. This insect, which was introduced, occurs in the northeastern states. Several undescribed species of Alucitidae are in North America.

SUPERFAMILY Pterophoroidea: The single family in Pterophoroidea occurs almost worldwide.

Family **Pterophoridae—Plume Moths**: These moths are small, slender, and usually gray or brownish and have the wings split into two or three featherlike divisions (Figure 30–52). The genus *Agdistis* is unusual in having no wing splits. The front wing usually has two divisions, and the hind wing three. The legs are relatively long. When at rest, the front and hind wings are folded close together and are held horizontally, at right angles to the body. The larvae of plume moths are leaf rollers and stem borers, and some occasionally do serious damage. The grape plume moth, *Geina periscelidactylus* (Fitch), is common on grape vines. The larvae tie together the terminal portions of the leaves and feed inside this shelter. Many plume moths have very spiny pupae. This is a fair-sized group, with 146 species in North America.

SUPERFAMILY Copromorphoidea: Superfamily Copromorphoidea is a relatively small group of more than 16 species, in two families.

Family **Copromorphidae**: This is a predominantly tropical group, with only five species occurring in the United States and Canada. They occur along the Pacific Coast from British Columbia to Mexico and east to Colorado. They are similar to the Carposinidae but differ in having all three branches of M present in the hind wing. The larva of *Lotisma trigonana* Walsingham is a fruit borer in *Arbutus* and *Gaultheria* (Ericaceae). The other species in the family are in the genus *Ellabella*.

Family **Carposinidae:** The moths in this group have relatively broad wings with raised scale tufts on the front wings, and there is no M_2 (and usually also no M_1) in the hind wings. This group is a small one, with only 11 species in North America. The larvae whose habits are known bore into fruits, plant shoots, and the gummy enlargements of fruit trees. The larvae of the currant fruitworm, *Carposina fernaldana* Busck, feed on the fruits of the currant. The infested fruit eventually drops, and the larvae pupate in the soil.

Family **Hyblaeidae**: These moths are similar to the Noctuidae but differ in having two distinct anal veins in the front wing. This is a tropical group, one species of which occasionally occurs in the southern states. This species is *Hyblaea puera* (Cramer), which has the front wings brownish and the hind wings yellowish with two dark-brown cross bands. It has a wingspread of about 26 mm. Hyblaeid larvae in Australia can regurgitate the contents of the gut and squirt them several centimeters when disturbed.

SUPERFAMILY Thyridoidea: Thyridoids lack abdominal tympana and have naked tongues, characters that separate them from the Pyraloidea. Their larvae share with hyblaeids the ability to eject the contents of the gut.

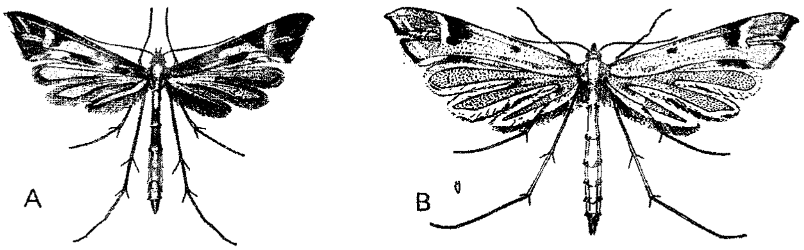

Figure 30–52 Plume moths (Pterophoridae). A, *Stenoptilodes baueri* (Lange), female; B, *S. grandis* (Walsingham), female; 2×. (Courtesy of Lange and Hilgardia.)

Family **Thyrididae—Window-Winged Moths:** The thyridids are often small and dark-colored and have clear spaces in the wings (Figure 30–40F). All branches of the radius are present, and they arise from the usually open discal cell (Figure 30–23A). Some larvae burrow in twigs and stems and cause gall-like swellings. Others feed on flowers and seeds. The most common eastern species is probably *Dysodia ocultana* Clemens, which occurs in the Ohio Valley. *Dysodia* larvae form leaf rolls with a faint but noticeable foul smell. Some tropical species are more colorful, and a few of these may occur in the Florida Keys.

SUPERFAMILY Pyraloidea—Snout and Grass Moths: The superfamily Pyraloidea is the third largest in the order, with more than 1,375 species occurring in the United States and Canada. Most pyraloids are small and rather delicate moths, and all have abdominal tympanal organs and a scaled proboscis. The front wings are elongate or triangular, with the cubitus appearing four-branched and the hind wings usually broad. Veins Sc and R in the hind wing are usually close together and parallel opposite the discal cell (the base of R is usually atrophied), and are fused or closely parallel for a short distance beyond the discal cell (Figure 30–15). Because the labial palps are often projecting, these moths are sometimes called "snout moths."

The members of this superfamily vary greatly in appearance, venation, and habits. The superfamily consists of two families, which are divided into a number of subfamilies, only a few of which can be mentioned here.

Family **Pyralidae:** In this family the praecinctorium is absent and the tympanal case is closed medially. Representative North American subfamilies are Galleriinae, Chrysauginae, Pyralinae, Epipaschiinae, and Phycitinae.

Subfamily Galleriinae: The best-known member of this subfamily is the bee moth or wax moth, *Galleria mellonella* (L.). The larva occurs in beehives, where it feeds on wax. It often does considerable damage. The adult has brownish front wings and a wingspread of about 25 mm.

Subfamily Pyralinae: This subfamily (27 North American species) is a group of small moths. The larvae of most species feed on dried vegetable matter. One of the most important species in this subfamily is the meal moth, *Pyralis farinalis* L. The larva feeds on cereals, flour, and meal and makes silken tubes in these materials. The larvae of the clover hayworm, *Hypsopygia costalis* (Fabricius), live in old stacks of clover hay.

Subfamily Phycitinae: The subfamily is a large one (about 400 North American species), and most of the members have long, narrow front wings and broad hind wings. The larvae vary considerably in habits. The best-known species in this subfamily are those that attack stored grain: the Indian meal moth, *Plodia interpunctella* (Hübner), and the Mediterranean flour moth, *Anagasta kuehniella* (Zeller). The former is a gray moth with the apical two thirds of the front wings dark brown, and the latter is uniformly gray (Figure 30–53). Both moths are rather small. The larvae of the Indian meal moth feed on cereals, dried fruits, meal, and nuts and spin webs over these materials. They often cause enormous losses in stored food supplies. The Mediterranean flour moth attacks all types of grain products and is an important pest in granaries, warehouses, markets, and homes.

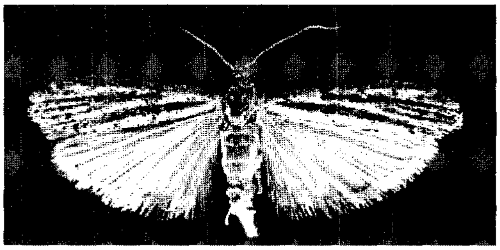
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Figure 30–53 The Mediterranean flour moth, *Anagasta kuehniella* (Zeller), 4×.

The cactus moth, *Cactoblastis cactorum* (Berg), has been introduced into Australia to control the prickly pear cactus. This moth has successfully destroyed the dense cactus growth over many square miles of territory in New South Wales and Queensland. It now occurs in the southern United States (Florida, Georgia, South Carolina), probably as an accidental introduction.

Several species of *Dioryctria* bore into the cambium of the trunk, branches, and shoots and in the fresh cones of pines and other conifers. They are especially damaging to ornamentals and forest plantations, and the species attacking cones are probably the most damaging of the insect pests of forest tree seeds.

Another interesting species in this subfamily is the coccid-eating pyralid, *Laetilia coccidivora* Comstock, the larva of which is predaceous on the eggs and young of various scale insects.

Family **Crambidae:** In this family the praecinctorium is present and the tympanum is open mesally. Subfamilies present in North America are the Scopariinae, Crambinae, Schoenobiinae, Cybalomiinae, Nymphulinae, Evergestinae, Glaphyriinae, and Pyraustinae.

Subfamily Crambinae—Close-Wings or Grass Moths: These are common moths in meadows, where the larvae (known as "sod webworms") bore into the stems, crowns, or roots of grasses. Most feed about the base of grasses, where they construct silken webs. The moths are usually whitish or pale yellowish brown and, when at rest, hold the wings close about the body (hence the

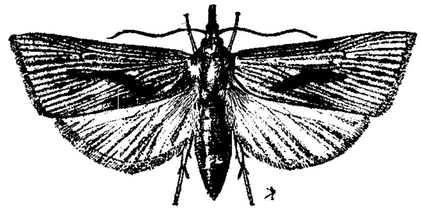

Figure 30–54 The sugarcane borer, *Diatraea saccharalis* (Fabricius) (Crambidae, Crambinae), 2×. (Courtesy of USDA.)

name "close-wing"). An important pest species in this subfamily is the sugarcane borer, *Diatraea saccharalis* (Fabricius) (Figure 30–54), the larva of which bores in the stalks of sugarcane. Most species in this group belong to the genus *Crambus* and related genera.

Subfamily Nymphulinae: The larvae of most Nymphulinae are aquatic, often breathing by means of gills and feeding on aquatic plants. The water lily leaf cutter, *Synclita obliteralis* (Walker), lives on greenhouse water plants, in cases made of silk. Adult females dive underwater to lay eggs.

Subfamily Pyraustinae: The subfamily is a large group (more than 375 North American species), and many of its members are relatively large and conspicuously marked. The most important species in this subfamily is the European corn borer, *Ostrinia nubilalis* (Hübner), which was introduced into the United States about 1917 and has since spread over a large part of the central and eastern states. The larvae live in the stalks of corn and other plants and frequently do a great deal of damage. This species has one or two generations a year. It overwinters in the larval stage. The adult moths (Figure 30–55) have a wingspread of a little over 25 mm and are yellowish brown with darker markings.

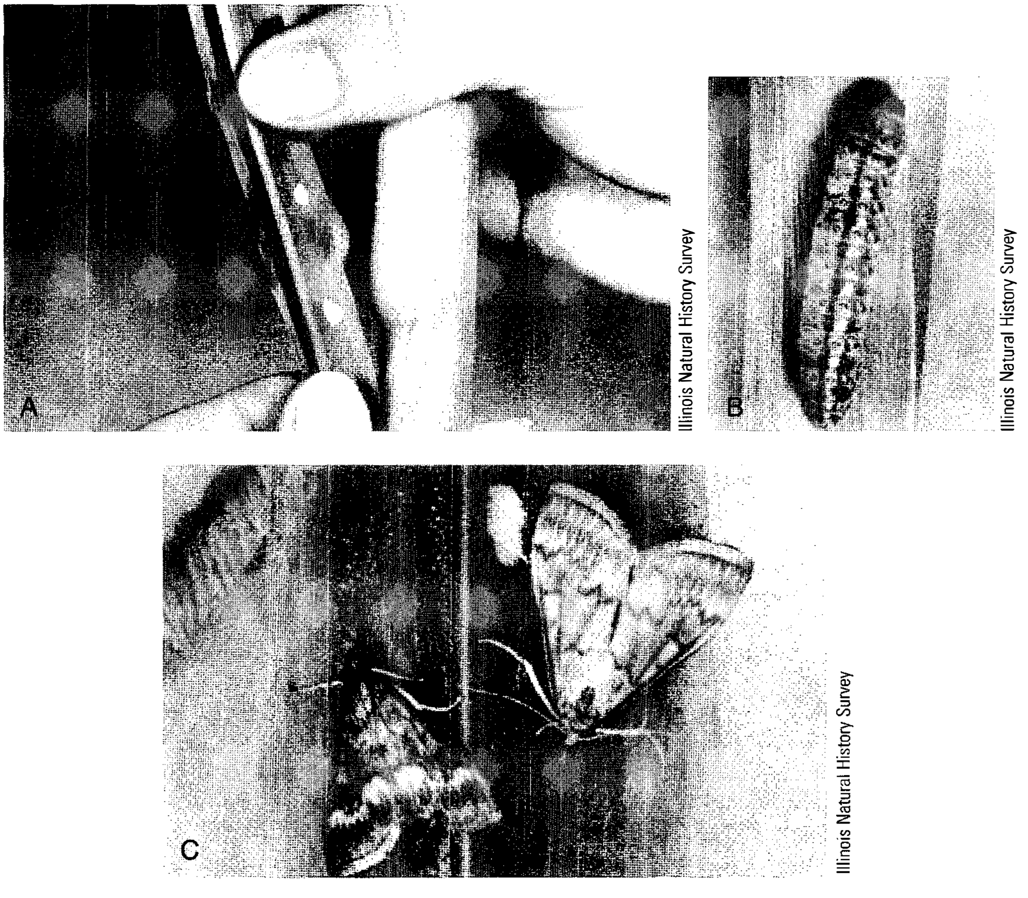

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Figure 30–55 The European corn borer, *Ostrinia nubilalis* (Hübner). A, egg masses on corn; B, larva; C, adults (male at left, female at right); 2×.

The grape leaf folder, *Desmia funeralis* (Hübner), is a black moth with two white spots in the front wing and one white spot in the hind wing. The larva feeds on grape leaves, folding the leaf over and fastening it with silk. The melonworm, *Diaphania hyalinata* (L.), is a glistening white moth with the wings bordered with black (Figure 30–40A). The larva is primarily a foliage feeder on melons and related plants. Other important species in this subfamily are the pickleworm, *Diaphania nitidalis* (Stoll), and the garden webworm, *Achyra rantalis* (Guenée).

SUPERFAMILY Hesperioidea: The single family Hesperiidae is included in this superfamily.

***Family* Hesperiidae—Skippers:** The skippers are for the most part small and stout-bodied, and they get their name from their fast and erratic flight. They differ from the butterflies (Papilionoidea) in that none of the five R branches in the front wings are stalked, and all arise from the discal cell (Figure 30–8). The antennae are widely separated at the base, and the tips are usually recurved or hooked (Figure 30–7B). Most skippers at rest hold the front and hind wings at a different angle. The larvae are smooth, with the head large and the neck constricted. They usually feed inside a leaf shelter, and pupation occurs in a cocoon made of leaves fastened together with silk. Most species overwinter as larvae, either in leaf shelters or in cocoons.

Nearly 300 species of skippers occur in North America. Most, including all the eastern species, belong to two subfamilies, the Pyrginae (Hesperiinae of some authors) and the Hesperiinae (the Pamphilinae of some authors). Two other subfamilies, the Pyrrhopyginae and Heteropterinae, occur in the South and Southwest.

Subfamily Pyrrhopyginae: These skippers have the antennal club wholly reflexed; that is, the tip of the antenna is bent back before the club. This group is principally tropical, but one species, *Pyrrhopyge araxes* (Hewitson), occurs in southern Texas and Arizona. This is a large (wingspread 45–60 mm), dark-colored skipper with light spots in the front wings, and the wings are held horizontally when at rest. The larvae feed on oak.

Subfamily Pyrginae: In the front wings of the Pyrginae, the discal cell is usually at least two thirds as long as the wing. M_2 arises midway between M_1 and M_3 and is not curved at the base (Figure 30–8A). The middle tibiae lack spines. The males of some species have a costal fold, a long, slitlike pocket near the costal margin of the front wing, which serves as a scent organ. Some species have scale tufts on the tibiae. Most skippers in this group are relatively large grayish or blackish insects (Figure 30–56A,E,F).

One of the largest and most common species in this subfamily is the silver-spotted skipper, *Epargyreus*

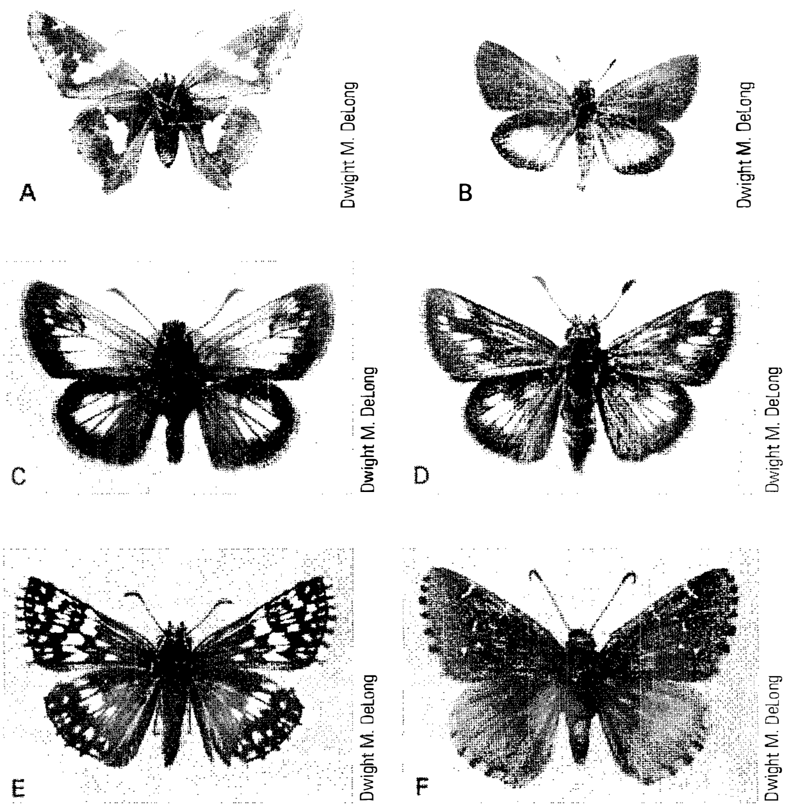

Figure 30–56 Skippers (Hesperiidae). **A**, the silverspotted skipper, *Epargyreus clarus* (Cramer) (Pyrginae), underside of wings, natural size; **B**, the least skipper, *Ancyloxipha numitor* (Fabricius) (Hesperiinae), 1½×; **C**, the Hobomok skipper, *Poanes hobomok* (Harris) (Hesperiinae), 1½×; **D**, Peck's skipper, *Polites peckius* (Kirby) (Hesperiinae); **E**, checkered skipper, *Pyrgus communis* (Grote) (Pyrginae), 1½×; **F**, the northern cloudy wing, *Thorybes pylades* (Scudder) (Pyrginae), slightly enlarged.

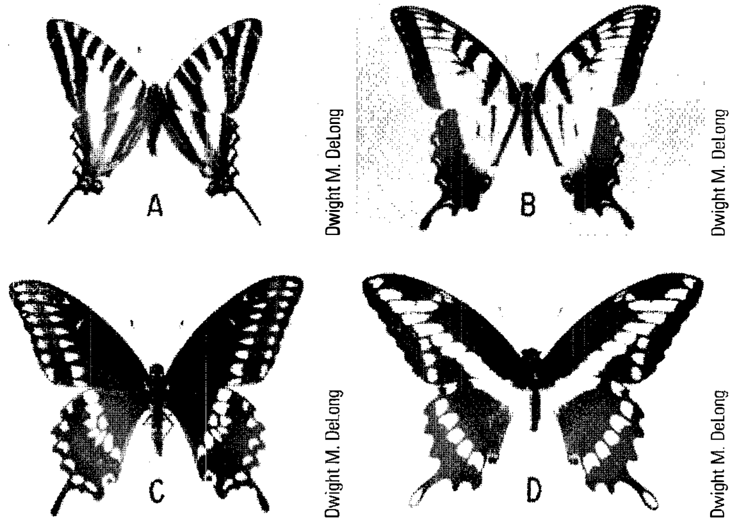

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Figure 30–57 Swallowtail butterflies. A, the zebra swallowtail, *Eurydites marcellus* (Cramer); B, the tiger swallowtail, *Papilio glaucus* L.; C, the black swallowtail, *Papilio polyxenes asterius* Stoll, male; D, the giant swallowtail, *Papilio cresphontes* Cramer. About one third natural size.

clarus (Cramer). It is dark brown with a large yellowish spot in the front wing and a silvery spot on the underside of the hind wing (Figure 30–56A). The larva feeds on black locust and related plants. The species overwinters as a pupa.

Subfamily **Heteropterinae:** This group is represented in North America by only five species (one in the genus *Carterocephalus* and four in the genus *Piruna*), and they are seldom encountered.

Subfamily **Hesperiinae—Tawny Skippers, Giant Skippers:** In these skippers the discal cell in the front wings is less than two thirds as long as the wing. M_2 in the front wings is usually curved at the base and arises nearer to M_3 than to M_1 (Figure 30–8B). The middle tibiae are often spined. The tawny skippers (Figure 30–56B–D) are usually brownish, with an oblique dark band (often called the *stigma* or *brand*) across the wing of the males. This dark band consists of scales that serve as outlets for the scent glands. Giant skippers have a wingspread of 40 mm or more, and the antennal club is not recurved as in most other skippers. Giant skippers are stout-bodied and fast-flying. When at rest, they hold the wings vertically above the body. The larvae bore in the stems and roots of yucca and related plants. Maguey worms are the larvae of a giant skipper.

SUPERFAMILY **Papilionoidea—Butterflies:** Characters of the thorax unite the four families that have about 560 species in North America. Their large size, often conspicuous color patterns, and diurnal habits make butterflies a prominent element North American insect fauna.

Family **Papilionidae—Swallowtails and Parnassians:** Two subfamilies of papilionids occur in North America, the Papilioninae and the Parnassiinae. These are sometimes given family rank. The Papilioninae (swallowtails) are large, usually dark-colored butterflies that have the radius in the front wing five-branched and usually have one or more tail-like prolongations on the rear side of the hind wing (Figure 30–57). The Parnassiinae (parnassians) are medium-sized and usually white or gray with dark markings (Figure 30–58); the radius in the front wing is four-branched; and there are no tail-like prolongations on the hind wings.

Subfamily **Parnassiinae—Parnassians:** The parnassians are medium-sized butterflies that are usually white or gray with dark markings on the wings (Figure 30–58). Most have two small, reddish spots in the hind wings. These butterflies pupate on the ground, among fallen leaves, in loose, cocoonlike structures. After mating, the male secretes a hard-drying substance over the genital opening of the female, thus preventing other males from inseminating the same female. The parnassians are principally montane and boreal in distribution.

Subfamily **Papilioninae—Swallowtails:** This group contains the largest and some of the most beautifully colored North American butterflies. In many species the two sexes are somewhat differently colored. This

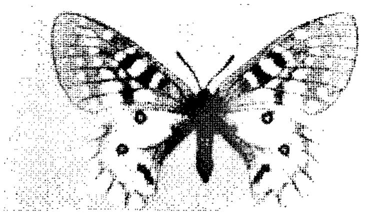

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Figure 30–58 A parnassian, *Parnassius clodius baldur* Edwards. About two thirds natural size.

group contains the largest butterflies in the world, the giant birdwings of southeast Asia and Australia, some of which have a wingspread of about 255 mm. The larvae are usually smooth-bodied and have an eversible scent gland or osmeterium (Figure 30–3, *osm*). This gland is everted from the upper part of the prothorax when the larva is disturbed, and gives off a disagreeable odor. Some larvae have markings like eyespots at the anterior end and resemble the head of a small vertebrate. This resemblance, together with the "forked tongue" appearance of the scent gland, makes them seem quite ferocious—though they are actually quite harmless. The chrysalis is attached to various objects by the cremaster and is held more or less upright by a silk girdle about the middle of the body (Figure 30–4A). The winter is passed in the chrysalis.

Swallowtails are widely distributed, but the following species are fairly common in the eastern states: The black swallowtail, *Papilio polyxenes asterius* Stoll (Figure 30–57C), is largely black, with two rows of yellow spots around the margin of the wings. The female has quite a bit of blue between the two rows of yellow spots in the hind wings. The larva feeds on carrot leaves, parsley, and related plants. The tiger swallowtail, *Papilio glaucus* L. (Figures 30–57B, 35–21), is a large, yellow swallowtail with black stripes in the front wings and black wing margins. In some individuals the wings are almost entirely black. The larva feeds on cherry, birch, poplar, and various other trees and shrubs. The spicebush swallowtail, *Papilio troilus* L., is blackish, with a row of small, yellowish spots along the margins of the front wings and extensive blue-gray areas in the rear half of the hind wings. The larva feeds on spicebush and sassafras. The zebra swallowtail, *Eurytides marcellus* (Cramer) (Figure 30–57A), is striped with black and greenish white and has relatively long tails. The larva feeds on pawpaw. This species shows considerable variation, because the adults emerging in different seasons differ slightly in their markings. The pipe-vine swallowtail, *Battus philenor* (L.), is largely black, with the hind wings shading into metallic green posteriorly. The larva feeds on Dutchman's-pipe. The giant swallowtail or orangedog, *Papilio cresphontes* Cramer (Figure 30–57D), is a large, dark-colored butterfly with rows of large, yellow spots on the wings. The larva feeds chiefly on citrus in the South and on prickly ash in the North.

Family **Pieridae—Whites, Sulphurs, and Orange-tips:** The pierids are medium-sized to small butterflies, usually white or yellowish in color with black marginal wing markings. The radius in the front wing is usually three- or four-branched (rarely five-branched in some orange-tips). The front legs are well developed, and the tarsal claws are bifid. The chrysalids are elongate and narrow and are attached by the cremaster and by a silken girdle around the middle of the body. Many pierids are very common and abundant butterflies and are sometimes seen in mass migrations.

The 63 North American species of pierids are arranged in three subfamilies, the Pierinae (whites and orange-tips), Coliadinae (sulphurs or yellows), and Dismorphiinae. The Dismorphiinae are a tropical group, only one species of which occasionally gets into southern Texas.

Subfamily Pierinae—Whites and Orange-tips: These butterflies are usually white. There is usually a distinct humeral vein in the hind wing, and the third segment of the labial palps is long and tapering. One of the most common species in this group is the cabbage butterfly, *Pieris rapae* (L.) (Figure 30–59B), the larva of which often does considerable damage to cabbage and related plants. It has two or more generations a year and overwinters as a chrysalis. The pine butterfly, *Neophasia menapia* (Felder and Felder), is a white that is very destructive to ponderosa pine in the northwestern states.

Orange-tips are small, white butterflies with dark markings (Figure 30–59A). The underside of the wings is mottled with green, and the front wings of many species are tipped with orange. These butterflies are mainly western. Only two species occur in the East, and they are relatively rare. The larvae feed on cruciferous plants.

Subfamily Coliadinae—Sulphurs or Yellows: These pierids are yellow or orange and usually have the wings margined with black. Rarely, they may be white with black wing margins. The humeral vein in the hind wing is lacking (Figure 30–13B) or represented by just

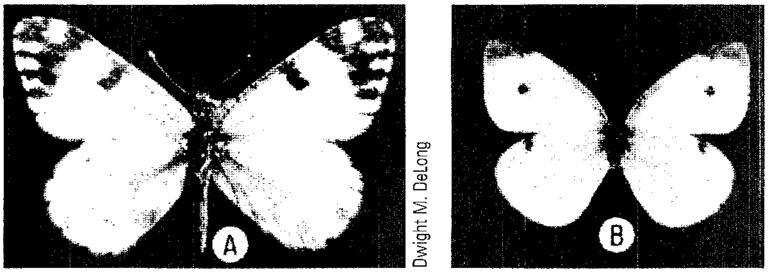

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Figure 30–59 Pierid butterflies. A, an orange-tip, *Euchloe creusa lotta* Beutenmüller; B, the cabbage butterfly, *Pieris rapae* (L.). A, slightly enlarged; B, slightly reduced.

a stub, and the third segment of the labial palps is short. Many species occur in two or more seasonal color forms. A common butterfly in this group is the orange sulphur or alfalfa butterfly, *Colias eurytheme* Boisduval. Most individuals of this species are orange with black wing margins, but some females are white. The larva feeds on clovers and related plants and often does serious damage to clover crops. The common or clouded sulphur, *C. philodice* Godart, is yellow with black margins. It often can be found in large numbers around muddy pools along roadsides. The larva feeds on clovers. The females of these sulphurs have a broader black marginal band on the wings than do the males, and there are light spots in this band, particularly in the front wings.

***Family* Lycaenidae—Coppers, Hairstreaks, Blues, Harvesters, and Metalmarks:** These are small, delicate, and often brightly colored butterflies, and some are quite common. The body is slender, the antennae are usually ringed with white, and a line of white scales encircles the eyes. The radius in the front wing is three- or four-branched (three-branched in some Lycaeninae, four-branched otherwise). M_1 in the front wing arises at or near the anterior apical angle of the discal cell (except in some Miletinae, see Figure 30–60A), and there is no humeral vein in the hind wing (except in the Riodininae; Figures 30–12B, 30–14B, 30–60). The front legs are normal in the female, but are shorter and lack tarsal claws in the male. Lycaenid larvae are flattened and sluglike; many secrete honeydew, which attracts ants, and some live in ant nests. The chrysalids are fairly smooth and are attached by the cremaster, with a silken girdle about the middle of the body. The adults are rapid fliers.

The approximately 160 North American species of Lycaenidae are arranged in three subfamilies, Riodininae, Miletinae (Gerydinae, Liphyrinae), and Lycaeninae (Polyommatinae, Theclinae).

Subfamily Riodininae—Metalmarks: The metalmarks are small, dark-colored butterflies that differ from other lycaenids in having the costa of the hind wing thickened out to the humeral angle and in having a short humeral vein in the hind wing (Figure 30–14A). Most species in this group are tropical or western, and only three occur in the East. The little metalmark, *Calephelis virginiensis* (Guérin-Méneville), with a wingspread of about 20 mm, occurs in the southern states, and the northern metalmark, *Calephelis borealis* (Grote and Robinson) (Figure 30–61D), with a wingspread of 25–30 mm, occurs as far north as New York and Ohio. The little metalmark is fairly common in the South, but the northern metalmark is quite rare. The larvae feed on ragwort, thistle, and other plants.

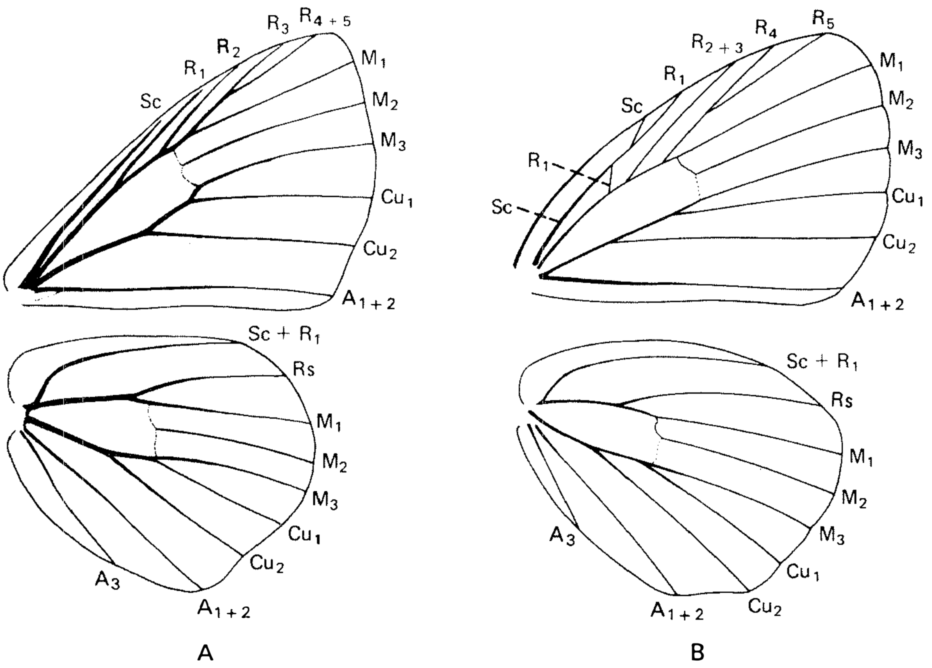

Figure 30–60 Wings of Lycaenidae. A, harvester (Miletinae); B, blue (Lycaeninae).

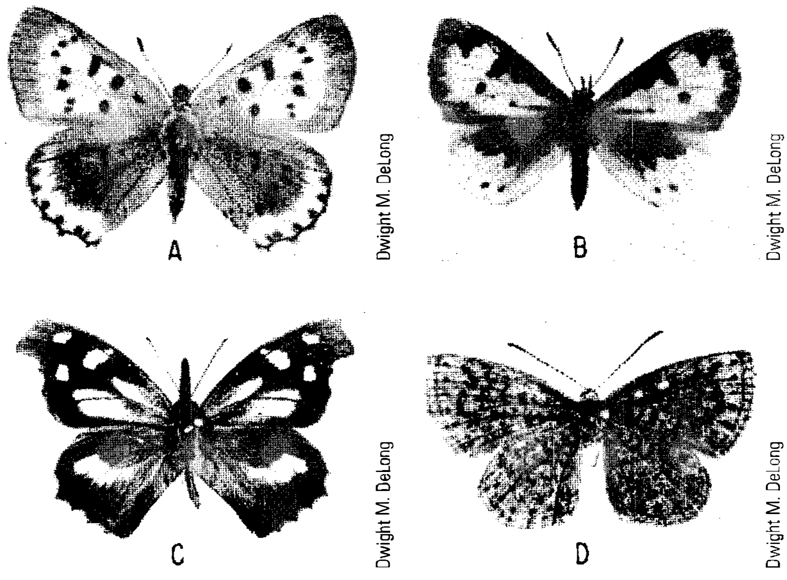

Figure 30–61 A, the American copper, *Lycaena phlaeas americana* Harris (Lycaenidae, Lycaeninae); B, the harvester, *Feniseca tarquinius* (Fabricius) (Lycaenidae, Miletinae); C, a snout butterfly, *Libytheana bachmanii* (Kirtland) (Nymphalidae, Libytheinae); D, the northern metalmark, *Calephalis borealis* (Grote and Robinson) (Lycaenidae, Riodininae). A, B, and D, slightly enlarged; C, about natural size.

Subfamily Miletinae—Harvesters: The harvesters differ from the other lycaenids in having M_1 in the front wings stalked with a branch of R for a short distance beyond the discal cell (Figure 30–60A). The wanderer or harvester, *Feniseca tarquinius* (Fabricius), is the only member of this group occurring in the United States. It is a brownish butterfly with a wingspread of about 25 mm (Figure 30–61B). The larva is predaceous on aphids and is one of the few predaceous lepidopteran larvae. This species is rather local and uncommon and (despite its name) does very little wandering.

Subfamily Lycaeninae—Coppers, Hairstreaks, Blues: The coppers are small butterflies that are orange-red or brown (often with a coppery tinge) with black markings. The last branch of R in the front wings (R_{3-5}) is forked (with the branches R_3 and R_{4+5}) and arises at the anterior apical angle of the discal cell (Figure 30–14B). These butterflies generally live in open areas such as marshes and meadows and along roadsides.

The American copper, *Lycaena phlaeas americana* Harris (Figure 30–61A), is one of the most common species in this group. The adults are quite pugnacious and often "buzz" other butterflies (and even collectors!). The larva feeds on dock (*Rumex*).

The hairstreaks are usually dark gray or brownish, with delicate striping on the underside of the wings and usually with small, reddish spots in the posterior part of the hind wings. Usually the hind wings have two or three hairlike tails. There are only three branches of R in the front wing, and the last one is simple (Figure 30–12B). These butterflies have a swift, darting flight and are commonly found in meadows, along roadsides, and in other open areas.

One of the most common eastern species is the gray hairstreak, *Strymon melinus* Hübner. The larva bores in the fruits and seeds of legumes, cotton, and other plants. The great purple hairstreak, *Atlides halesus* (Cramer), is the largest eastern species, with a wingspread of a little over 25 mm. It is brilliantly colored—blue, purple, and black—and quite iridescent. It occurs in the southern states. The elfins (*Incisalia*) are small, brownish, early spring species that lack tails but have scalloped edges of the hind wings.

The blues are small, delicate, slender-bodied butterflies whose upper surface of the wings is often blue. The females are usually darker than the males, and some species occur in two or more color forms. The last branch of R in the front wing is forked (as in the coppers), but arises a little proximad of the anterior apical angle of the discal cell (Figure 30–60B). Many larvae secrete honeydew, to which ants are attracted.

One of the most common and widespread species in this group is the spring azure, *Celastrina argiolus* (L.). This species exhibits considerable geographic and seasonal variation in size and coloring. The tailed blues (*Everes*) have delicate, tail-like prolongations on the hind wings.

***Family* Nymphalidae—Brush-Footed Butterflies:** This is a fairly large group (about 210 North American species) and includes many common butterflies. The common name of the family refers to the fact that the front legs are much reduced and lack claws, and only the middle and hind legs are used in walking. The chrysalids are usually suspended by the cremaster (Figure 30–4B). This family is divided into eight subfamilies.

Subfamily Libytheinae—Snout Butterflies: These small, brownish butterflies have long, projecting palps. The males have reduced front legs, with only the middle and hind legs used in walking, whereas the females have longer front legs and use them in walking. One species, *Libytheana bachmanii* (Kirtland), is common and widely distributed. This is a reddish brown butterfly with white spots in the apical part of the front wings and with the outer margin of the front wings rather deeply notched (Figure 30–61C). The larva feeds on hackberry.

Subfamily Heliconiinae—Heliconians, Fritillaries: The heliconians differ from other nymphalids in having the humeral vein in the hind wing bent basad (Figure 30–12A) and the front wings relatively long and narrow (Figure 30–62). This group is largely tropical, and only five species occur in the United States. The most common U.S. heliconian is the zebra butterfly, *Heliconius charitonius* (L.), a black butterfly striped with yellow (Figure 30–62A). This species occurs in the Gulf States, but it is most common in Florida. The chrysalis, when disturbed, wriggles about in a characteristic manner. A heliconian that occurs over a large part of the southeastern United States, extending as far north as New Jersey and Iowa and with a southwestern subspecies extending into southern California, is the gulf fritillary, *Agraulis vanillae* (L.). This butterfly is bright orange-brown with black markings (Figure 30–62B). The butterflies in this group appear to have distasteful body fluids and are avoided by predators. The larvae feed on various species of passionflowers.

The fritillaries are brownish butterflies with numerous black markings consisting principally of short, wavy lines and dots. The underside of the wings is often marked with silvery spots. Most larger fritillaries belong to the genus *Speyeria* (Figure 30–63B). *Speyeria* larvae are nocturnal and feed on violets. The smaller fritillaries, 25–40 mm in wingspread, belong principally to the genus *Boloria*. Their larvae also feed on violets and other plants.

Subfamily Nymphalinae—Anglewings, Crescents, and Checkerspots: These butterflies have hairy eyes, and the hind wing is angled or tailed at the end of M_3. The anglewings (*Polygonia*) are small to medium-sized and brownish with black markings. The wings are irregularly notched and often bear tail-like projections, and the distal half of the rear edge of the front wing is somewhat excavated (Figure 30–63F). The underside of the wings is darker and looks much like a dead leaf, and there is usually a small C-shaped silvery spot on the underside of the hind wing. The larvae feed principally on nettles, elm, hopvines, and other Urticaceae. The mourning cloak, *Nymphalis antiopa* (L.), is a common butterfly that is brownish-black with yellowish wing margins (Figure 30–63D); the larvae are gregarious and feed chiefly on willow, elm, and poplar. This is one of the few butterflies that overwinters in the adult stage, and the adults appear early in the spring.

Crescents and checkerspots are small butterflies (wingspread mostly 25–40 mm) in which the eyes are bare and the palps are densely hairy beneath. The crescents (*Phyciodes*) are small, brownish butterflies with black markings, and the wings (particularly the front wings) are margined with black (Figure 30–63C). They have a wingspread of about 25 mm. The larvae feed principally on asters. The checkerspots (*Chlosyne*) are similar to the crescents, but they are usually a little larger, and the darker areas on the wings are generally more extensive. The larvae feed on asters and related plants.

Another group of nymphalids (sometimes placed in the subfamily Vanessinae) has the eyes hairy, but the margin of the hind wing is rounded, not angled or tailed at the end of M_3. This group includes the red ad-

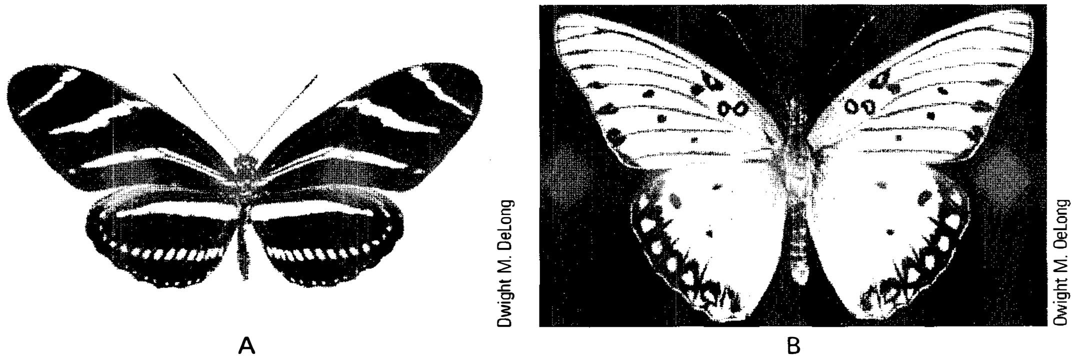

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Figure 30–62 Heliconian butterflies (Nymphalidae, Heliconiinae). A, the zebra butterfly, *Heliconius charitonius* (L.); B, the gulf fritillary, *Agraulis vanillae* (L.). Slightly reduced.

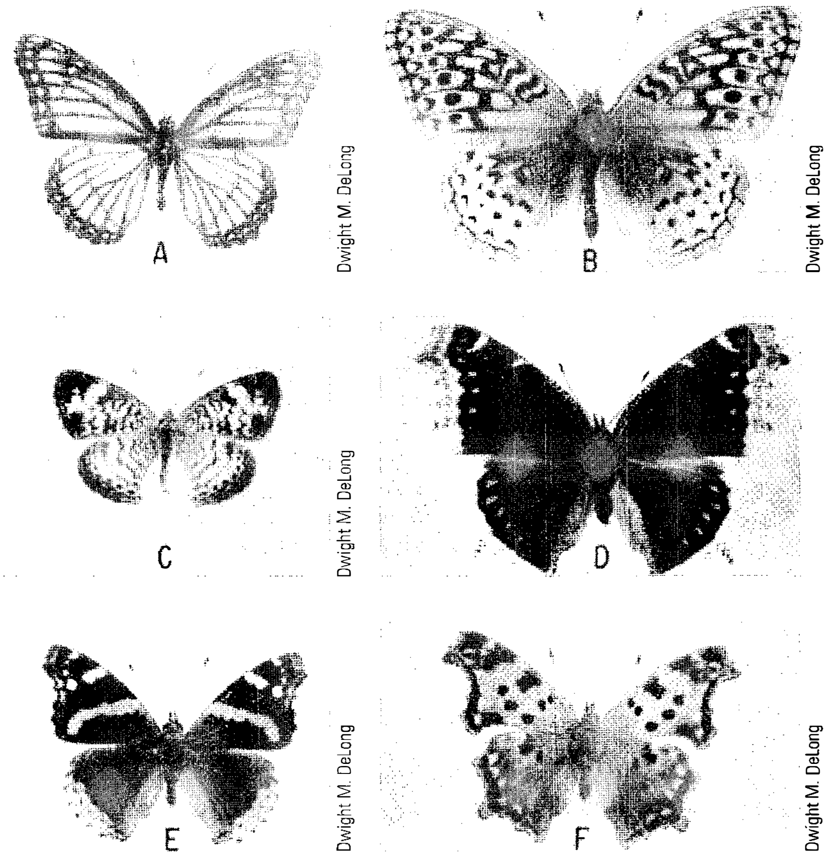

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Figure 30–63 Brush-footed butterflies (Nymphalidae). A, the viceroy, *Limenitis archippus* (Cramer); B, the great spangled fritillary, *Speyeria cybele* (Fabricius); C, the pearl crescent, *Phyciodes tharos* Drury; D, the mourning cloak, *Nymphalis antiopa* (L.); E, the red admirable, *Vanessa atalanta* (L.); F, the comma, *Polygonia comma* (Harris). C, about natural size; the others slightly reduced.

miral, *Vanessa atalanta* (L.) (Figure 30–63E), a very common and widely distributed butterfly. The larva feeds principally on nettles, feeding in a shelter formed by tying a few leaves together. There are usually two generations a year. Two very similar and fairly common species in this group are the painted lady, *V. cardui* (L.), and Hunter's butterfly, *V. virginiensis* (Drury). These butterflies are orange-brown and brownish black above, with white spots in the front wings. The painted lady has four small eyespots on the underside of each hind wing, and Hunter's butterfly has two large eyespots on the underside of each hind wing. The larva of the painted lady feeds chiefly on thistles, whereas that of Hunter's butterfly feeds on everlastings.

Subfamily Limenitidinae—Admirals, Viceroy, and Others: The members of this group are medium-sized butterflies in which the antennal club is long, and the humeral vein in the hind wing arises opposite the origin of Rs (Figure 30–11B). The viceroy, *Limenitis archippus* (Cramer), is a common species in this group that looks very much like the monarch. It differs in that it is slightly smaller, has a narrow black line across the hind wings, and has only a single row of white spots in the black marginal band of the wings (Figure 30–63A). The resemblance of the viceroy to the monarch is a good example of protective (or Batesian) mimicry. The monarch is "protected" by distasteful body fluids and is seldom attacked by predators, and the viceroy's resemblance to the monarch is believed to provide it with at least some protection from predators. The larva of the viceroy, a rather grotesque-looking caterpillar, feeds on willow, poplar, and related trees. It overwinters in a leaf shelter formed by tying a few leaves together with silk. The red-spotted purple, *L. arthemis astyanax* (Fabricius), another common species in this group, is a blackish butterfly with pale bluish or greenish spots and with reddish spots on the underside of the wings. The larva, which is similar to that of the viceroy, feeds on willow, cherry, and other trees, and it overwinters in a leaf shelter. A similar butterfly, the banded purple, *L. arthemis arthemis* (Drury), occurs in the northern states. It has a broad white band across the wings.

Subfamily Charaxinae—Goatweed Butterflies: Four species of *Anaea* occur in the central and southwestern parts of the United States. The larvae feed on *Croton* (Euphorbiaceae).

Subfamily Apaturinae—Hackberry Butterflies and Emperors: These butterflies are somewhat similar to the painted lady, but the dark areas in the front wings are brownish rather than black, and the eyes are bare. The larvae feed on hackberry, and adults are generally found around these trees.

Subfamily Satyrinae—Satyrs, Wood Nymphs, and Arctics: These butterflies are small to medium-sized, usually grayish or brown, and they generally have eyelike spots in the wings. The radius of the front wings is five-branched, and some of the veins in the front wings (particularly Sc) are considerably swollen at the base (Figure 30–10B). The larvae feed on grasses. The chrysalis is usually attached by the cremaster to leaves and other objects.

One of the most common species in this group is the wood nymph, *Cercyonis pegala* (Fabricius), a dark brown, medium-sized butterfly with a broad, yellowish band across the apical part of the front wing. This band contains two black-and-white eyespots (Figure 30–64A). Another common species is the little wood satyr, *Megisto cymela* (Cramer), a brownish-gray butterfly with prominent eyespots in the wings and with a wingspread of about 25 mm (Figure 30–64C). The pearly eye, *Enodia portlandia* (Fabricius) (Figure 30–64D), a brownish butterfly with a row of black eyespots along the border of the hind wings, is a woodland species with a quick flight and a habit of alighting on tree trunks. Among the most interesting species in this group are the arctics or mountain butterflies (*Oeneis*), which are restricted to the arctic region and the tops of high mountains. A race of the melissa arctic, *O. melissa semidea* (Say), is restricted to the summits of the White Mountains in New Hampshire, and a race of the polixenes arctic, *O. polixenes katahdin* (Newcomb), occurs on Mount Katahdin in Maine. The jutta arctic, *O. jutta* (Hübner) (Figure 30–64B), is a wide-ranging circumpolar species that occurs farther south than do most other arctics. It may be found in the sphagnum bogs of Maine, New Hampshire, and Michigan in alternate years.

Subfamily Danainae—Milkweed Butterflies: The danaines are large and brightly colored butterflies, usually brownish with black and white markings. The front legs are very small, without claws, and are not used in walking. The radius in the front wing is five-branched; the discal cell is closed by a well-developed vein; and there is a short third anal vein in the front wing (Figure 30–10A). The larvae feed on milkweed. The chrysalids are hung by the cremaster to leaves or other objects. The adults are "protected" by distasteful body fluids, and are seldom attacked by predators.

The most common species in this group is the monarch butterfly, *Danaus plexippus* (L.), which occurs throughout the United States and a large part of the remainder of the world. The monarch is an orange butterfly with the wings bordered by black. In most of the black marginal band, there are two rows of small white spots (Figure 30–65A). The caterpillar is yellowish green banded with black, with two threadlike appendages at either end of the body (Figure 30–65B). The chrysalis is pale green spotted with gold.

The monarch is one of the few butterflies that migrates (see Chapter 4). Large numbers migrate south in the fall, and the species reappears in the north the following spring. The longest flight known for an adult

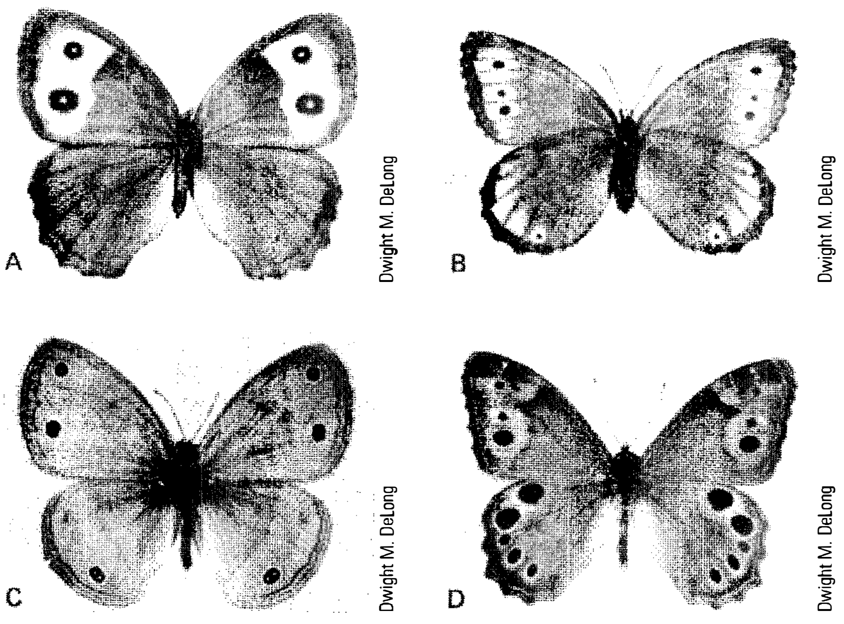

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Figure 30–64 Satyrid butterflies. **A**, a wood nymph, *Cercyonis pegala* (Fabricius); **B**, the jutta arctic, *Oeneis jutta* (Hübner); **C**, the little wood satyr, *Megisto cymela* (Cramer); **D**, the pearly eye, *Enodia portlandia* (Fabricius). **A**, slightly reduced; **C**, slightly enlarged; **B** and **D**, about natural size.

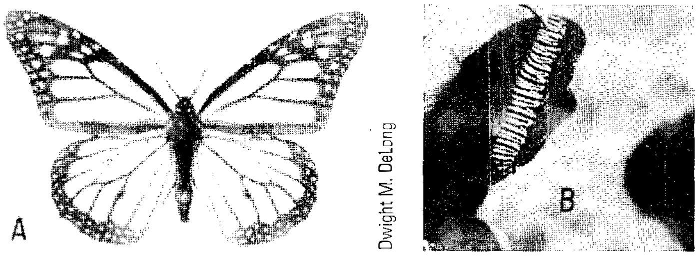

Figure 30–65 The monarch, *Danaus plexippus* (L.). A, adult male; B, larva. About one half natural size.

monarch (based on a tagged individual) is more than 1,800 miles (2,900 km), from Ontario to Mexico. The butterflies that migrate south in the fall overwinter in the south and usually start back north the following spring. They may reproduce in their wintering grounds or after a short northward flight in the spring. The butterflies that arrive in the northern United States in the summer are not the same individuals that left there the preceding fall but are the offspring of individuals that reproduced in the wintering grounds or en route north (see Urquhart 1960). After two summer generations in the north, the fall generation returns to the same wintering grounds in Mexico, even though it is three generations removed from that of the previous winter. The principal wintering grounds for the monarch are in Mexico, but some winter in Florida (or Cuba) and in southern California.

The queen, *Danaus gilippus* (Cramer), a common species in the southeastern states, is similar to the monarch but is darker and lacks the dark lines along the veins. Its larva also feeds on milkweed. A subspecies of the queen occurs in the Southwest.

Family **Drepanidae:** The two subfamilies in this group have adults that are very different in appearance. The hook-tip moths (Drepaninae) are small, slender, and usually dull colored and can generally be recognized by the sickle-shaped apex of the front wings. Internal abdominal tympanal organs are present. The cubitus in the front wings appears four-branched; in the hind wing, $Sc+R_1$ and Rs are separated along the discal cell; and the frenulum is small or absent. The larvae feed on the foliage of various trees and shrubs. The most common species in this group is *Drepana arcuata* Walker, a dirty white moth marked with dark brownish lines and with a wingspread of about 25 mm (Figure 30–66A). It occurs in the Atlantic states. This group is a small one, with only five species in North America.

The species of the subfamily Thyatirinae are similar to the Noctuidae, but they have the cubitus appearing three-branched in the front wings and four-branched in the hind wings, and the veins $Sc+R_1$ and Rs in the hind wings are more or less parallel along the anterior margin of the discal cell. They have abdominal rather than thoracic tympanal organs. The larvae of this small group (16 North American species) feed on various trees and shrubs.

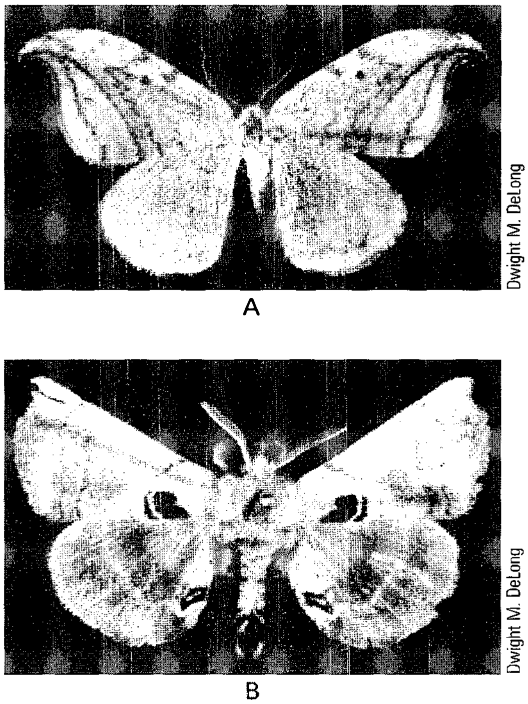

Figure 30–66 A, a hook-tip moth, *Drepana arcuata* Walker, 2×; B, an apatelodid moth, *Apatelodes torrefacta* (J. E. Smith), 1½×.

SUPERFAMILY **Geometroidea:** Three families make up the Geometroidea. Two have abdominal tympanal organs, and all have naked proboscises.

***Family* Sematuridae:** This family is represented in the United States by a single species, *Anurapteryx crenulata* Barnes and Lindsey, a Mexican species that ranges into Arizona. It is the only family of the Geometroidea that lacks abdominal tympana.

***Family* Uraniidae:** The uraniids have veins R_5 and M_1 stalked and separate from R_4 on the fore wing. The subfamily Uraniinae is a tropical group, most species of which are brightly colored and day-flying. A single species, *Urania fulgens* (Walker), has been reported in Texas. This Neotropical species resembles a swallowtail butterfly. It is blackish with pale, metallic, greenish bands on the wings and the tails of the hind wings whitish, and it has a wingspread of 80–90 mm.

The subfamily Epipleminae is a small group of moths that are similar in size and general appearance to the Geometridae but differ in wing venation. They have Sc+R and Rs in the hind wing widely separated from near the base of the wing. The cubitus in the front wing appears to have three branches. The larvae have sparse hair and five pairs of prolegs. Eight species of this group occur in the United States. The moths are plain colored and have a wingspread of about 20 mm.

***Family* Geometridae—Measuringworms, Loopers, Geometers:** This family is the second largest in the order, with some 1,400 species occurring in the United States and Canada. The moths in this family are mostly small, delicate, and slender-bodied. The wings are usually broad and often marked with fine, wavy lines. The two sexes are often different in color, and in a few species the females are wingless or have only rudimentary wings. The geometers are principally nocturnal and are often attracted to lights. The most characteristic feature of the wing venation is the form of the subcosta in the hind wing (Figure 30–20). The basal part of this vein makes an abrupt bend into the humeral angle and is usually connected by a brace vein to the humeral angle. The cubitus in the front wing appears to have three branches. This family, like all the Geometroidea except the Sematuridae, has tympanal organs on the abdomen.

The larvae of geometers are the familiar caterpillars called "inchworms" or "measuringworms" (Figure 30–67). They have two or three pairs of prolegs at the posterior end of the body and none in the middle. Locomotion is accomplished by placing the posterior end of the body near the thoracic legs and then moving the anterior end of the body, thus progressing in a characteristic looping fashion. Many measuringworms, when disturbed, stand nearly erect on the posterior prolegs and remain motionless, resembling small twigs.

North American Geometridae are divided into six subfamilies: Archiearinae, Oenochrominae, Ennominae, Geometrinae, Sterrhinae, and Larentiinae. The largest is the Ennominae, which includes about half of the North American species. It differs from the other subfamilies in having M_2 in the hind wings weak or absent (Figure 30–20B).

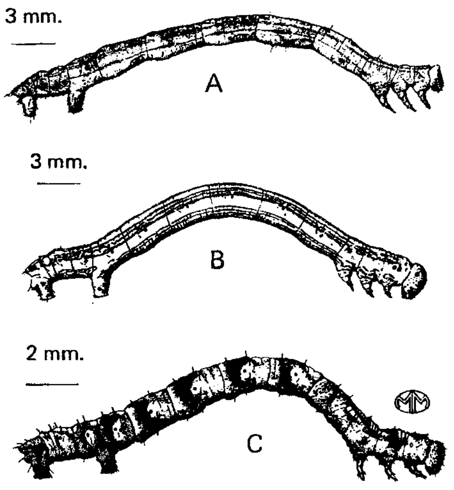

Figure 30–67 Larvae of Geometridae. A, *Pero morrisonarius* (H. Edwards); B, *Nepytia canosaria* (Walker); C, *Protoboarmia porcelaria indicatoria* Walker. (Courtesy of McGuffin and MacKay, and The Canadian Entomologist.)

This family contains the cankerworms, which feed on the foliage of various deciduous trees and often cause serious defoliation. The two common species are the spring cankerworm, *Paleacrita vernata* (Peck) (Ennominae), and the fall cankerworm, *Alsophila pometaria* (Harris) (Oenochrominae) (Figure 30–68). The spring cankerworm overwinters in the pupal stage, and the female lays its eggs in the spring. The fall cankerworm overwinters in the egg stage. The larvae of the spring cankerworm have two pairs of prolegs; the larvae of the fall cankerworm have three pairs. The adult females of both species are wingless.

Many geometers are common moths, but only a few can be mentioned here. The chickweed geometer, *Haematopis grataria* (Fabricius) (Sterrhinae), is a reddish yellow moth with the margins of the wings and two bands near the margins pink (Figure 30–69B). It has a wingspread of about 25 mm or less, and the larva feeds on chickweed. One of the largest moths in this family is the notch-wing geometer, *Ennomos magnarius* Guenée (Ennominae). It has a wingspread of 35–50 mm. The wings are reddish yellow with small, brown spots, and they shade to brown toward the outer margin (Figure 30–69A). The larvae feed on various trees. Many geometers are light green. One of the common species of this type is the bad-wing, *Dyspteris abortivaria* (Herrich-Schäffer) (Larentiinae) (Figure 30–69D). The front wings are large and triangular, and the hind wings

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Figure 30–68 The fall cankerworm, *Alsophila pometaria* (Harris). A, adult female laying eggs; B, adult male. Natural size.

are small and rounded. This moth has a wingspread of a little less than 25 mm. The larva rolls and feeds on grape leaves.

Several members of this family are important forest pests. The hemlock looper, *Lambdina fiscellaria* (Guenée) (Ennominae), is a widely distributed species attacking hemlock and other conifers, and it has occurred in outbreak numbers. The adults resemble those of *Ennomos magnarius* (Figure 30–69A). The mountain mahogany looper, *Anacamptodes clivinaria profanata* (Barnes and McDunnough) (Ennominae), feeds on mountain mahogany (*Cercocarpus*) and bitterbrush (*Purshia*) in the Northwest and is very destructive to both.

A European species in the subfamily Ennominae, *Biston betularia* (L.), is an example of the phenomenon known as *industrial melanism*. In areas of Great Britain where heavy industry covers tree trunks with soot, the light-colored individuals of this moth have been replaced by dark variants, which elsewhere are relatively rare. The dark forms have a better chance of escaping predation when alighting on soot-covered tree trunks than do the light-colored form.

SUPERFAMILY Mimallonoidea: The only family in this group is the Mimallonidae. They are mainly Neotropical.

***Family* Mimallonidae—Sack-bearers:** These insects are called "sack-bearers" because the larvae make cases from leaves and carry them about. The group is a small one, with 4 North American species in three genera (*Lacosoma, Naniteta*, and *Cicinnus*). The moths in the genus *Lacosoma* are yellowish in color and about 25 mm in wingspread, with the distal margin of the front wings deeply scalloped (Figure 30–70A). Those in the

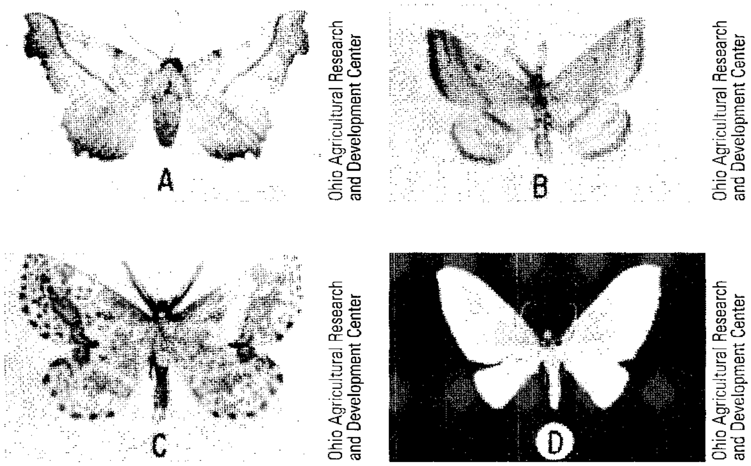

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Figure 30–69 Geometer moths. A, the notch-wing geometer, *Ennomos magnarius* Guenée; B, the chickweed geometer, *Haematopis grataria* (Fabricius); C, the crocus geometer, *Xanthotype sospeta* Drury; D, the bad-wing, *Dyspteris abortivaria* Herrick-Schäffer. A, slightly reduced; B, and D, slightly enlarged; C, about natural size.

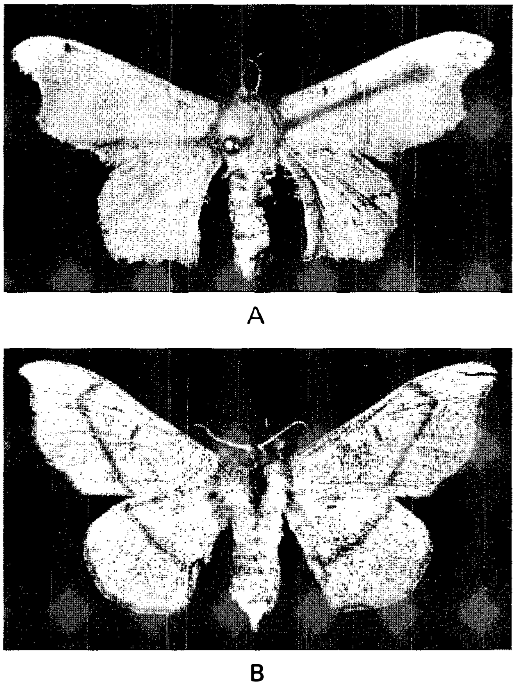

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Figure 30–70 Sackbearer moths (Mimallonidae). A, *Lacosoma chiridota* Grote, 2½×; B, *Cicinnus melsheimeri* Harris, 1½×.

genus *Cicinnus* are reddish gray peppered with small black dots and with a narrow dark line across the wings, a wingspread of about 32 mm, and the distal margin of the front wings evenly rounded (Figure 30–70B). The one species of *Naniteta*, *N. elassa* Franclemont, occurs in the Southwest.

SUPERFAMILY **Lasiocampoidea**: The single family is mainly Neotropical in distribution.

***Family* Lasiocampidae—Tent Caterpillars, Lappet Moths, and Others**: These moths are of medium size and have stout bodies, with the body, legs, and eyes hairy. The antennae are somewhat feathery in both sexes, but the processes on the antennae are longer in the male. There is no frenulum, and the humeral angle of the hind wing is expanded and provided with humeral veins (Figure 30–23B). Most of these moths are brown or gray in color. The larvae feed on the foliage of trees, often causing serious damage. Pupation occurs in a well-formed cocoon. Thirty-five species of lasiocampids occur in North America.

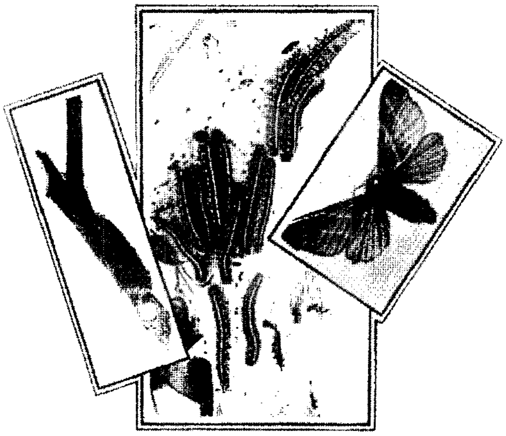

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Figure 30–71 The eastern tent caterpillar, *Malacosoma americanum* (Fabricius). Left, egg mass; center, larvae; right, adult female. ½×.

The eastern tent caterpillar, *Malacosoma americanum* (Fabricius) (Figure 30–71), is a common member of this group in eastern North America. The adults are yellowish brown. They appear in midsummer and lay their eggs in a bandlike cluster around a twig. The eggs hatch the following spring. The young that hatch from a given egg cluster are gregarious and construct a tentlike nest of silk near the eggs (Figure 30–72). This tent is used as a shelter, with the larvae feeding in nearby branches. The larvae feed on a number of dif-

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Figure 30–72 Tents of the eastern tent caterpillar.

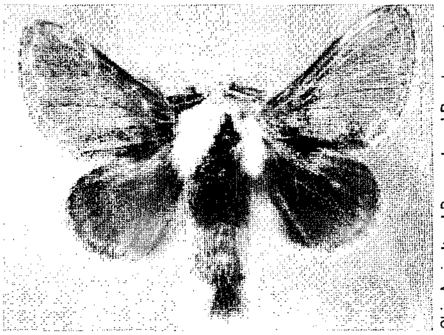

Figure 30–73 A lappet moth, *Tolype vellida* (Stoll) (Lasiocampidae). About natural size.

ferent trees, but seem to prefer cherry. The larvae are black and somewhat hairy and have a yellow stripe down the middle of the back. When full grown, they wander off and spin their cocoons in sheltered places.

The forest tent caterpillar, *Malacosoma disstria* Hübner, is widely distributed, but is probably more common in the South and Southwest where it sometimes defoliates large areas. The larvae differ from those of the eastern tent caterpillar in that they have a row of keyhole-shaped spots (rather than a stripe) down the middle of the back. The adults are somewhat paler than those of the eastern tent caterpillar.

The lappet moths (*Tolype*) are bluish gray with white markings (Figure 30–73). The common name refers to the fact that the larvae have a small lobe or lappet on each side of each segment. The larvae of *T. vellida* (Stoll) feed on apple, poplar, and lilac, and those of *T. laricis* (Fitch) feed on larch. The two species of *Artace* in North America are common in the South and Southwest. They are similar to *Tolype* but are white with black dots.

The largest North American lasiocampids are species of *Gloveria*, some of which have a wingspread of 80 mm. They occur in the Southwest, and their larvae feed on the foliage of trees and shrubs, especially oaks and *Ceanothus*.

SUPERFAMILY Bombycoidea: The moths of superfamily Bombycoidea have the prothoracic coxae of the last-instar larva fused anteriorly, have setae D1 of A8 arising from a mesal protuberance, and have R_2+R_3 closely parallel to or fused with the stem of R_4+R_5 on the fore wing.

***Family* Bombycidae—Silkworm Moths:** Only a single species of the subfamily Bombycinae occurs in North America, the silkworm, *Bombyx mori* (L.). This native of Asia is occasionally reared in the United States. This insect has long been reared for its silk, and it is one of the most important beneficial insects. After centuries of domestication, it is now a domestic species and probably does not exist in the wild. Many different varieties of silkworms have been developed by breeding. About a hundred species are in this subfamily, most of which occur in Asia.

The adult moth is creamy white with several faint, brownish lines across the front wings, and it has a wingspread of about 50 mm. The body is heavy and very hairy. The adults do not feed, they rarely fly, and usually they live only a few days. Each female lays 300–400 eggs. The larvae are naked, have a short anal horn, and feed principally on mulberry leaves. They become full grown and spin their cocoons in about six weeks. When used for commercial purposes, the pupae are killed before they emerge, because the emergence of the moth breaks the cocoon fibers. Each cocoon consists of a single thread about 914 meters long. About 3,000 cocoons are used to make a pound of silk.

Sericulture is practiced in Japan, China, Spain, France, Italy, and Brazil. It was introduced into the South Atlantic states in colonial times but did not succeed. The silk has a commercial value of $200 million to $500 million annually.

Subfamily Apatelodinae: This subfamily is represented in North America by five species (in two genera, *Apatelodes* and *Olceclostera*). These moths are similar to the Notodontidae but usually have windowlike dots near the apex of the front wings. They have a wingspread of 40–50 mm (Figure 30–66B). The larvae feed on various shrubs and trees and pupate in the ground.

***Family* Saturniidae—Giant Silkworm Moths and Royal Moths:** This family includes the largest moths in North America, and some of the largest lepidopterans in the world. The largest moths in North America (*Hyalophora*) have a wingspread of about 150 mm or more, and some tropical species of *Attacus* have a wingspread of about 250 mm. The smallest saturniids in North America have a wingspread of about 25 mm. Many members of this family are conspicuously or brightly colored, and many have translucent eyespots in the wings. The antennae are feathery (bipectinate or quadripectinate) for about half or more of their length and are larger in the male than in the female. The mouthparts are reduced, and the adults do not feed. The females produce a sex pheromone that males can detect from long distances. Many species fly mostly during the daylight hours or at dusk.

The larvae of saturniids (Figures 30–74, 30–75B) are large caterpillars, and many are armed with conspicuous tubercles or spines. Most (Saturniinae and most Hemileucinae) pupate in silken cocoons that are attached to the twigs or leaves of trees and shrubs or that are formed among leaves on the ground. Some (Ceratocampinae and some Hemileucinae) pupate in

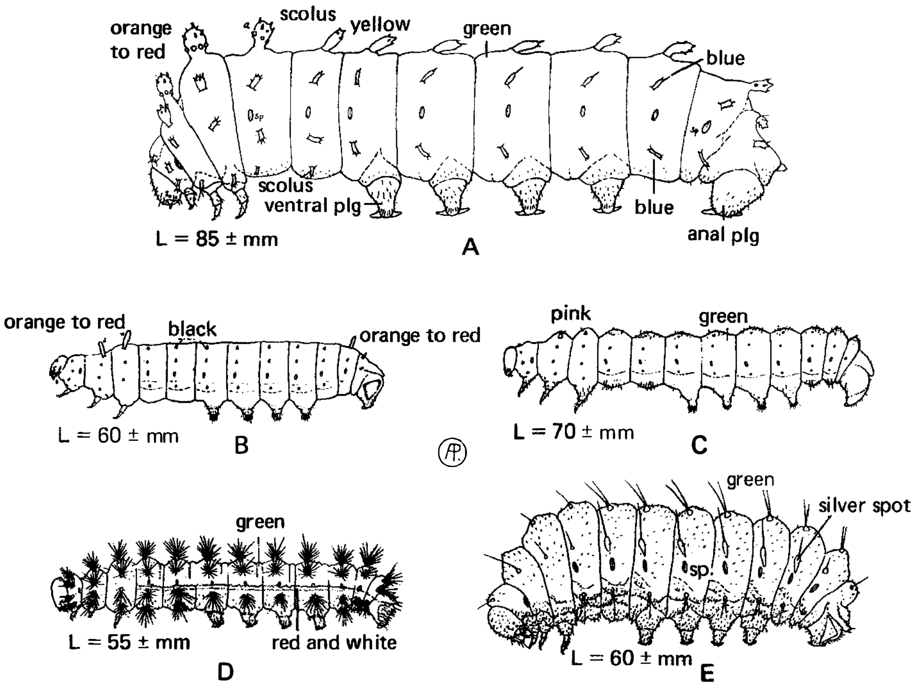

Figure 30–74 Larvae of Saturniidae. A, cecropia, *Hyalophora cecropia* (L.); B, promethea, *Callosamia promethea* (Drury); C, luna, *Actias luna* (L.); D, io, *Automeris io* (Fabricius); E, polyphemus, *Antheraea polyphemus* (Cramer). *plg*, proleg. (Courtesy of Peterson; reprinted by permission.)

the ground without forming a cocoon. Most species overwinter in the pupal stage and have one generation a year. A few species in this group have been used for the production of commercial silk. Some of the Asiatic species have provided a silk that makes strong and long-wearing fabrics, but none of the North American species has proved satisfactory for commercial silk production.

The 68 North American species of saturniids are arranged in three subfamilies, the Ceratocampinae, the Hemileucinae, and the Saturniinae.

Subfamily Ceratocampinae—Royal Moths: The members of this group have two anal veins in the hind wing; the discal cell in the front wing is closed; and M_2 in the front wing is stalked with R for a short distance (Figure 30–22A). The antennae of the male are pectinate in the basal half only. The larvae are armed with horns or spines and pupate in the ground.

The largest North American member of this group is the regal or royal walnut moth, *Citheronia regalis* (Fabricius) (Figure 29–75A), which has a wingspread of 125–150 mm. The front wings are gray or olive-colored, spotted with yellow, and the veins reddish brown. The hind wings are orange-red, spotted with yellow; and the body is reddish brown with yellow bands. The larva (Figure 30–75B) is often called the "hickory horned devil." When full grown it is 100–130 mm long and has curved spines on the anterior part of its body. Although very ferocious in appearance, this caterpillar is quite harmless. It feeds principally on walnut, hickory, and persimmon.

The imperial moth, *Eacles imperialis* (Drury), is a large, yellowish moth with dark, peppered spots. Each wing has a pinkish brown diagonal band near the margin (Figure 30–75C). The larva feeds on various trees and shrubs. A related species from Mexico, *E. oslari* Rothschild, enters the United States in southern Arizona. The moths in the genus *Anisota* are small, with wingspreads of 25–40 mm. Most are brownish. The rosy maple moth, *Dryocampa rubicunda* (Fabricius), is pale yellow and banded with pink (Figure 30–75D).

Subfamily Hemileucinae: Some members of this group (*Automeris*) have one anal vein in the hind wing, whereas others have two. The discal cell in the front wing is usually closed (Figure 30–22B); M_1 in the front wing is usually not stalked with R; and the antennae of the males are pectinate to the tip. Most moths in this group have a wingspread of about 50 mm.

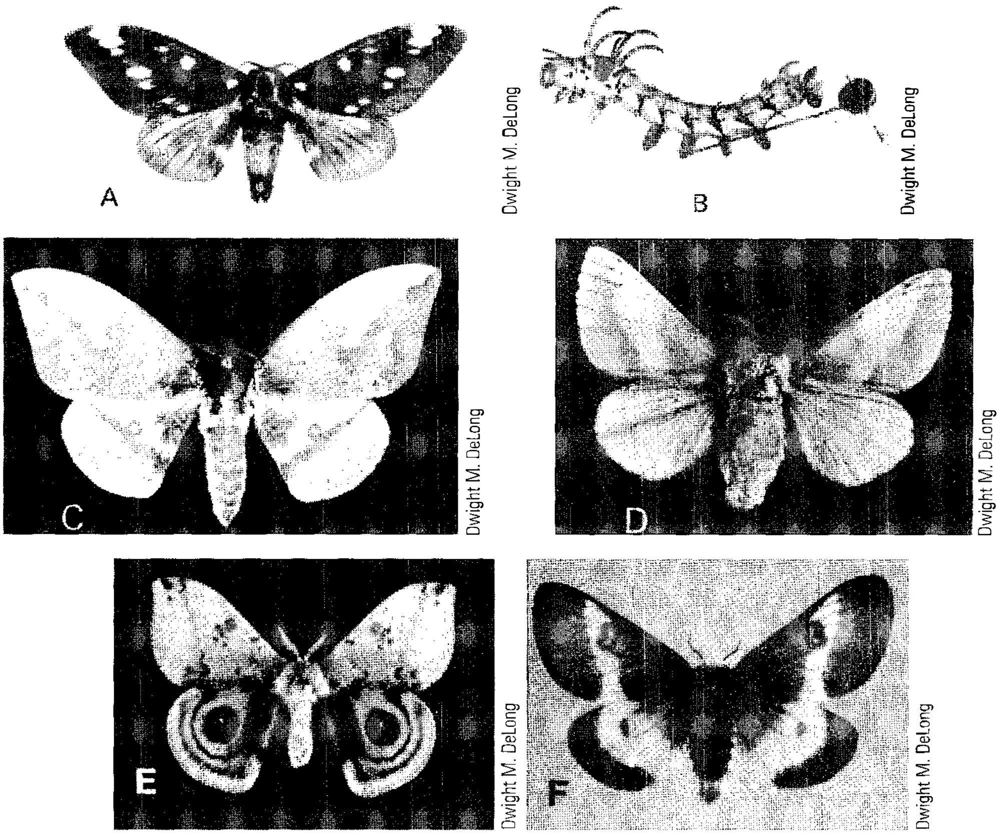

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Figure 30–75 Saturniid moths. A, adult, and B, larva of the regal moth, *Citheronia regalis* (Fabricius), $\frac{1}{2}\times$; C, the imperial moth, *Eacles imperialis* (Drury), $1\frac{1}{2}\times$; **D**, the rosy maple moth, *Dryocampa rubicunda* (Fabricius), slightly enlarged; E, the io moth, *Automeris io* (Fabricius), male, slightly reduced; F, the buck moth, *Hemileuca maia* (Drury), about natural size. A–D, Ceratocampinae; E–F, Hemileucinae.

The io moth, *Automeris io* (Fabricius), is one of the most common and the largest in this group. It has a wingspread of 50–75 mm and is yellow with a large eyespot in each hind wing (Figure 30–75E). The female is usually larger than the male, and its front wings are darker (reddish brown). The larva is a spiny green caterpillar with a narrow reddish stripe, edged below with white, extending along each side of the body (Figure 30–74D). Handle this larva with care, as the spines sting.

The buck moth, *Hemileuca maia* (Drury), is a little smaller than the io and is blackish with a narrow yellow band through the middle of each wing (Figure 30–75F). It occurs throughout the East; it is not commonly encountered, but can be locally abundant. It is largely diurnal in habit, and its larva (which has stinging hairs) pupates in the ground. *Hemileuca nevadensis* Stretch is a similar species occurring in the West. Its larva feeds on willow and poplar. Other species of *Hemileuca* feed on other trees or on grasses. Buck moths have a very rapid flight and are difficult to capture.

The pandora moth, *Coloradia pandora* Blake, a western species, is a little smaller than the io. It is gray with lighter hind wings, and it has a small, dark spot near the center of each wing. This species is an important defoliator of pines in the West.

Subfamily Saturniinae—Giant Silkworm Moths: The members of this subfamily have one anal vein in the hind wing; the discal cell of the front wing may be open (Figure 30–22C) or closed; and M_1 in the front wing is not stalked with R. The antennae of the male are pectinate to the tip.

The largest member of this subfamily in North America is the cecropia moth, *Hyalophora cecropia* (L.).

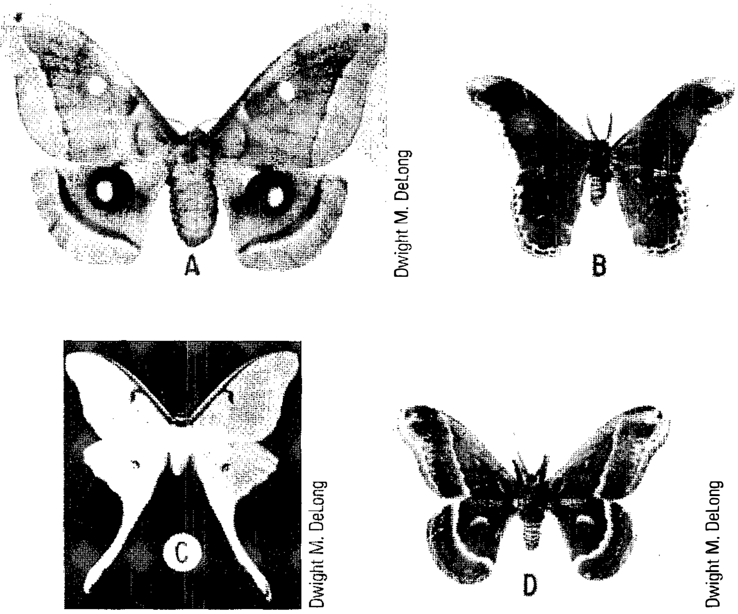

Figure 30–76 Giant silkworm moths (Saturniinae). A, the polyphemus, *Antheraea polyphemus* (Cramer); B, the promethea, *Callosamia promethea* (Drury); C, the luna, *Actias luna* (L.); D, the cecropia, *Hyalophora cecropia* (L.). A and B, ½×; C, ⅓×; D, ½×.

Most individuals have a wingspread of 130–150 mm. The wings are reddish brown, crossed a little distad of the middle by a white band. In the middle of each wing is a crescent-shaped white spot bordered with red (Figure 30–76D). The larva (Figure 30–74A) is a greenish caterpillar that reaches a length of about 100 mm. It has two rows of yellow tubercles down the back and two pairs of large red tubercles on the thoracic segments. The cocoons are formed on twigs. Three related and very similar species of *Hyalophora* occur in the West.

The promethea moth, *Callosamia promethea* (Drury), is sometimes called the "spicebush silk moth" because its larva feeds on spicebush, sassafras, and related plants. This moth is considerably smaller than the cecropia. The female is patterned a little like the cecropia, but the male (Figure 30–76B) is much darker, with a narrow, yellowish, marginal band of on the wings. Males fly during the afternoon and night and, when on the wing, look a little like a large mourning cloak butterfly. The cocoon is formed in a leaf. The larva prevents the leaf from falling off by securely fastening the petiole of the leaf to the twig with silk.

One of the most beautiful moths in this group is the luna moth, *Actias luna* (L.), a light green moth with long tails on the hind wings and with the costal border of the front wings narrowly bordered by dark brown (Figure 30–76C). The greenish larva (Figure 30–74C) feeds on walnut, hickory, and other trees, and forms its cocoon in a leaf on the ground.

Another common moth in this group is the polyphemus moth, *Antheraea polyphemus* (Cramer), a large, yellowish brown moth with a windowlike spot in each wing (Figure 30–76A). The larva (Figure 30–74E) is similar to that of the luna moth and feeds on various trees. Its cocoon is formed in a leaf on the ground.

Family **Sphingidae—Sphinx or Hawk Moths, Hornworms:** The sphinx moths are medium sized to large, heavy-bodied moths with long, narrow front wings (Figure 30–77). Some have a wingspread of 160 mm or more. The body is somewhat spindle shaped, tapering, and pointed both anteriorly and posteriorly. The antennae are slightly thickened in the middle or toward the tip. The subcosta and radius in the hind wing are connected by a crossvein (R_1) about opposite the middle of the discal cell (Figure 30–19B). The proboscis in many species is very long, sometimes as long as the body or longer. There are about 125 species of sphingids in North America.

These moths are strong fliers and fly with a very rapid wing beat. Some are day-fliers, but most are active at dusk or twilight. Most feed much like hummingbirds, hovering in front of a flower and extending their proboscis into it. These moths are in fact sometimes called "hummingbird moths," and in many species the body is about the size of a hummingbird. Some species (for example, *Hemaris*) have large areas in the wings devoid of scales and are called "clearwing sphinx moths." These are not to be confused with the clearwing moths of the family Sesiidae, which are smaller and more slender and have much more elongate front wings (compare Figures 30–77B and 30–46).

The name "hornworm" derives from the fact that the larvae of most species have a conspicuous horn or

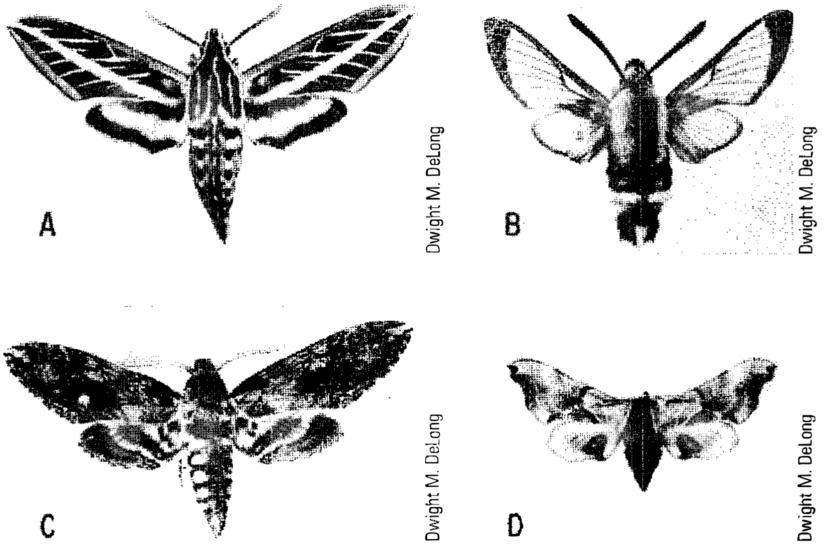

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Figure 30–77 Sphinx or hawk moths (Sphingidae). A, the white-lined sphinx, *Hyles lineata* (Fabricius); B, a clear-winged sphinx, *Hemaris diffinis* (Boisduval); C, adult of the tobacco hornworm, *Manduca sexta* (L.); D, the twin-spot sphinx, *Smerinthus jamaicensis* (Drury). A, C, and D, ½×; B, about natural size.

spinelike process on the dorsal surface of the eighth abdominal segment (Figure 30–78A). The name "sphinx" probably refers to the sphinxlike position that some of these larvae assume when disturbed. The larvae of most species pupate in the ground, in some cases forming pitcherlike pupae (proboscis of the pupa looks like a handle). Some species form a sort of cocoon among leaves on the surface of the ground.

One of the most common species in this group is the tomato hornworm, *Manduca quinquemaculata* (Haworth). The larva (Figure 30–78A) is a large, green caterpillar that feeds on tomato, tobacco, and potato. The larva of a similar species, *M. sexta* (L.), feeds on tobacco and other plants. The adults of these two species are large gray moths with a wingspread of about 100 mm. The hind wings are banded, and there are five (*quinquemaculata*) or six (*sexta*) orange-yellow spots along each side of the abdomen (Figure 30–77C). These hornworms often do considerable damage to the plants on which they feed. Hornworms are often attacked by braconid parasites, which form small, white, silken cocoons on the outside of the caterpillar (Figure 30–78B).

The largest North American sphingids (in terms of wing surface area) are females of the southwestern *Pachysphinx occidentalis* (Hy. Edwards), with a wingspread of up to 160 mm. A tropical species, *Cocytius antaeus* (Drury), which barely enters North America in southern Texas and Florida, can be even larger than *P. occidentalis*. The smallest North American sphingid is probably *Cautethia grotei* Hy. Edwards, which has a wingspread of just over 30 mm.

SUPERFAMILY Noctuoidea: All noctuoids have thoracic tympanal organs, which separate them from all other Lepidoptera.

***Family* Doidae:** Two southwestern species, *Doa ampla* (Grote) and *Leuculodes lecteolaria* (Hulst) represent this recently recognized family. The larvae of *D. ampla* feed on Euphorbiaceae.

***Family* Notodontidae (including Dioptidae, Heterocampidae)—Prominents and Oakworms:** The promi-

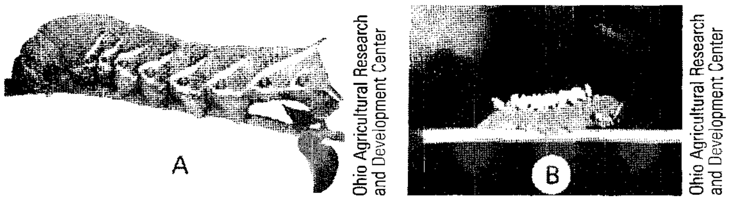

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Figure 30–78 A, the tomato hornworm, *Manduca quinquemaculata* (Haworth); B, a parasitized hornworm; the white objects on the back of this larva are cocoons of braconid parasites.

nents are usually brownish or yellowish moths that are similar to the Noctuidae in general appearance. The family and subfamily names (*not*-, back; -*odont*, tooth) refer to the fact that some species have backward-projecting tufts on the hind margin of the wings, which protrude when the wings are folded (they are usually folded rooflike over the body when at rest), and the larvae have conspicuous tubercles on the dorsal surface of the body. The prominents can be readily distinguished from the noctuids by the venation of the front wing (Figure 30–21B). In the Notodontidae, M_2 in the front wing arises from the middle of the apex of the discal cell, and the cubitus appears three-branched, whereas in the Noctuidae, M_2 in the front wing arises closer to M_3, and the cubitus appears four-branched (Figure 30–27). This family has nearly 140 North American species.

Notodontid larvae feed on various trees and shrubs and are often gregarious. When disturbed, they often elevate the anterior and posterior ends of the body and "freeze" in this position, remaining attached by the four pairs of prolegs in the middle of the body. The anal pair of prolegs is often rudimentary or modified into spinelike structures.

In this group, most of the brownish moths that have dark, narrow lines across the front wings belong to the genus *Datana*. These are sometimes called "handmaid moths" (Figure 30–79A). The larvae are blackish, with longitudinal yellow stripes. The yellow-necked caterpillar, *D. ministra* (Drury), feeds on apple and other trees. The walnut caterpillar, *D. intergerrima* Grote and Robinson, feeds principally on walnut and hickory.

The red-humped caterpillar, *Schizura concinna* (J. E. Smith), is a fairly common species in this group. The larva is black with yellow stripes, with the head and a hump on the first abdominal segment red (Figure 30–79B). The adult has a wingspread of a little over 25 mm. The front wings are gray with brown markings, and the hind wings are white with a small, black spot along the rear edge. The larva feeds on apple and other orchard trees and on various shrubs.

The oakworms are a New World group, most members of which occur in South America. Only two species occur in the United States. The only common species is the California oakworm, *Phryganidia californica* Packard, which occurs in California. The adults are slender moths, pale, translucent brown with dark veins, and have a wingspread of about 30 mm. The larvae feed on oak leaves and often do considerable damage.

***Family* Noctuidae:** This is the largest family in the order, with more than 2,900 species in the United States and Canada. These moths are mostly nocturnal in habit, and most moths attracted to lights at night belong to this family.

The noctuids are mostly heavy-bodied moths, with somewhat narrowed front wings and broadened hind wings (Figures 30–80, 30–81). The labial palps are usually long, the antennae are generally hairlike (sometimes brushlike in the males), and some species have tufts of scales on the dorsum of the thorax. The wing venation (Figures 30–24B, 30–27) is rather characteristic: M_2 in the front wing arises closer to M_3 than to M_1, and the cubitus appears to have four branches; the subcosta and radius in the hind wing are separate at the base but fuse for a short distance at the base of the discal cell; and M_2 in the hind wing may be present or absent.

Noctuid larvae are usually smooth and dull-colored (Figure 30–82), and most have five pairs of prolegs. The majority feed on foliage, but some are boring in habit and some feed on fruits. A number of species in this group are serious pests of various crops.

The noctuids have a pair of tympanal auditory organs located at the base of the metathorax. (Such organs are present in several other families of moths and are in some cases located on the abdomen.) These organs can detect frequencies of from 3 to more than 100 kHz,[3] and they appear to function in detecting and evading bats. Bats can detect prey (and obstacles) in complete darkness by means of a sort of sonar. They emit very high-pitched clicks (sometimes as high as 80 kHz) and locate objects from the echoes of these clicks.

The family Noctuidae is divided into a number of subfamilies, some of which have been given family

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[3] Three kilohertz is in the top octave of the piano; the average upper limit of hearing in humans is about 15 or 16 kHz.

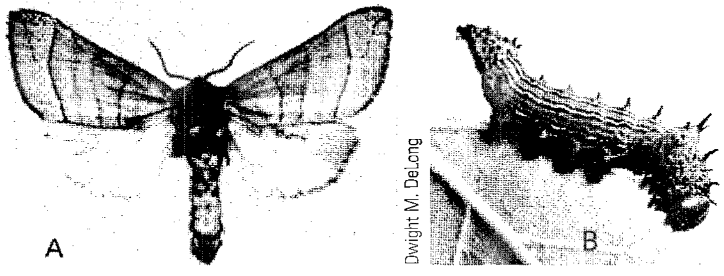

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Figure 30–79 Notodontidae. A, *Datana ministra* (Drury); B, the redhumped caterpillar, *Schizura concinna* (J. E. Smith). Natural size.

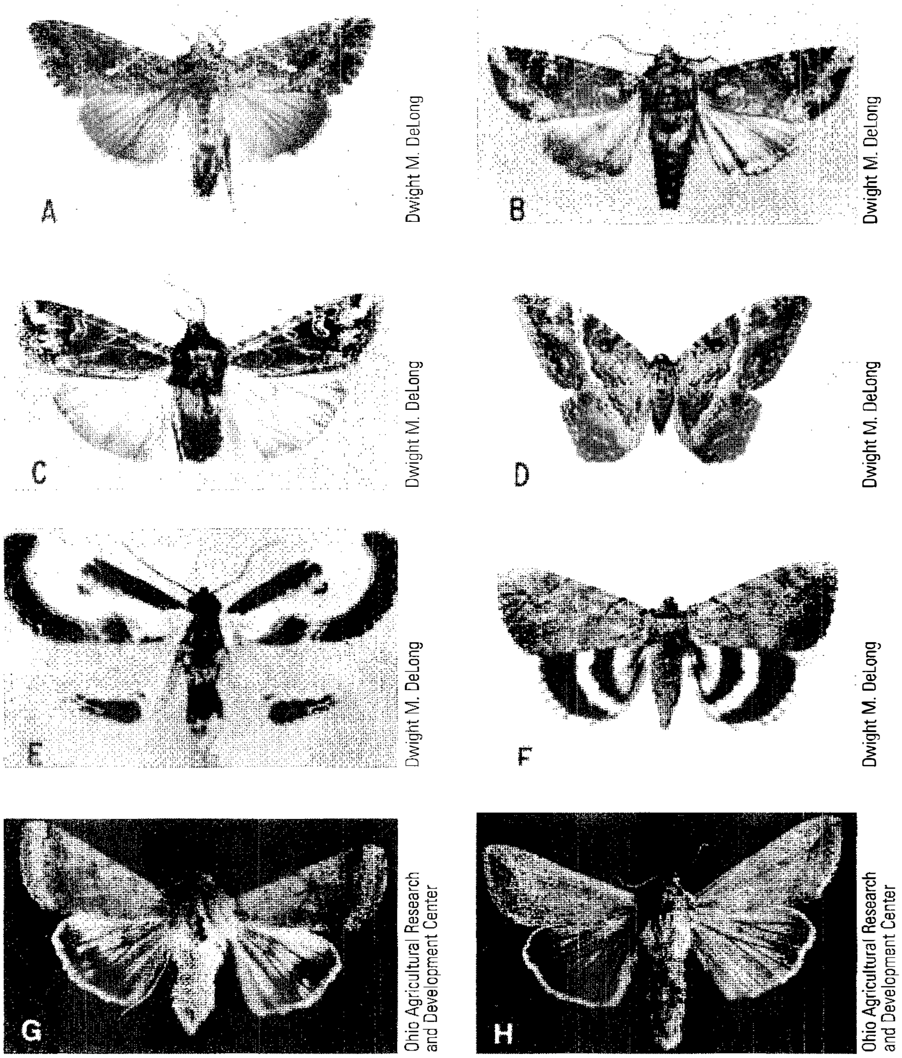

Figure 30–80 Noctuid moths. A, adult of the cabbage looper, *Trichoplusia ni* (Hübner); B, adult of the yellowheaded cutworm, *Apamea amputatrix* (Fitch); C, *Euxoa excellens* Grote (adult of one of the cutworms); D, the black witch, *Ascalapha odorata* (L.); E, *Euthisanotia grata* Fabricius; F, the darling underwing, *Catocala cara* Guenée; G, adult of the corn earworm, *Helicoverpa zea* (Boddie); H, adult of the armyworm, *Pseudaletia unipuncta* (Haworth). D, $\frac{1}{3}\times$; F, slightly reduced; the other figures approximately natural size.

rank. We make no attempt here to characterize all these subfamilies, and only mention a few.

Subfamilies Herminiinae, Strepsimaninae, and Hypeninae: These moths are the most primitive noctuids and are commonly called "quadrifids" (M_2 in the hind wing is well developed, and the cubitus thus appears four-branched). Many resemble pyralids, but they can be distinguished by their naked proboscis. *Nigetia formosalis* Walker (Strepsimaninae) is a rather pretty, mottled moth that is fairly common in the eastern United States.

Subfamily Catocalinae: This group includes the underwings, relatively large and strikingly colored moths of the genus *Catocala*. They are forest or woodland

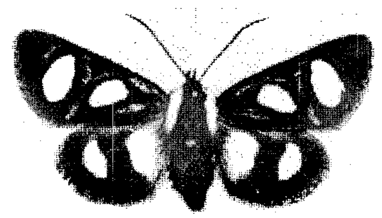

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Figure 30–81 The eight-spotted forester, *Alypia octomaculata* (Fabricius), 1½×.

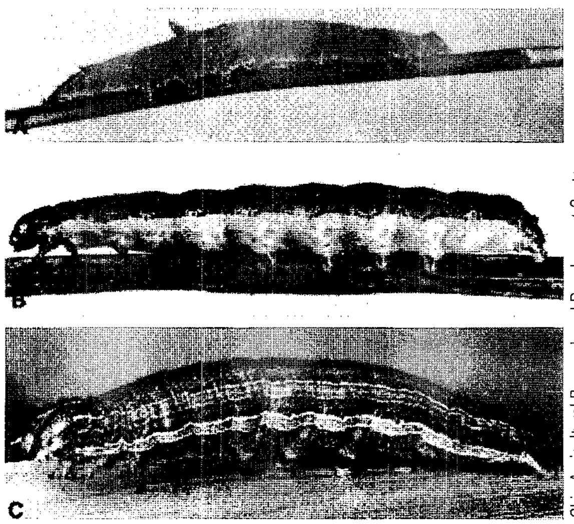

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Figure 30–82 Larvae of Noctuidae. A, *Catocala ultronia* Hübner (an underwing); B, the fall armyworm, *Spodoptera frugiperda* (J. E. Smith); C, the armyworm, *Pseudaletia unipuncta* (Haworth).

species, and their larvae feed on the foliage of various trees. The hind wings are usually brightly colored with concentric bands of red, yellow, or orange (Figure 30–80F). At rest, the hind wings are concealed, and the front wings are colored much like the bark of the trees on which these moths usually rest. This group includes the largest noctuid in the United States, the black witch, *Ascalapha odorata* (L.). This is a blackish species with a wingspread of 100–130 mm (Figure 30–80D). It breeds in the southern states, where the larvae feed on various leguminous trees. The adults sometimes appear in the northern states in late summer. *Ascalapha* and its relatives are sometimes placed in a separate subfamily, the Erebinae. Other Catocalinae include the large grass-feeding moths in the genus *Mocis*, which occur in the Southeast and in the tropics.

Subfamily Plusiinae—Loopers: These insects are called "loopers" because the larvae have only three pairs of prolegs and move like measuringworms. The cabbage looper, *Trichoplusia ni* (Hübner), is a serious pest of cabbage, and the celery looper, *Anagrapha falcifera* (Kirby), attacks celery. The adults of these loopers are dark brown, with a wingspread of about 35–40 mm, and have a small, elongate silver spot in the middle of each front wing (Figure 30–80A). Many plusiines have golden or silver metallic markings in the front wings.

Subfamily Acontiinae: This group contains some of the most colorful noctuids. *Cydosia nobilitella* (Cramer) is a common species in the Southeast and is often confused with ermine moths in the genus *Atteva*. Species of *Spragueia* are also common in the East and are usually a mottled orange and black. The small moths of the genera *Tripudia* and *Cobubatha* of the Southeast are often confused with tortricids. They can be easily distinguished by their thoracic tympanal organs.

Subfamily Agaristinae—Forester Moths: The foresters are usually black with two whitish or yellowish spots in each wing, and they have a wingspread of about 25 mm. The antennae are slightly clubbed. The eight-spotted forester, *Alypia octomaculata* (Fabricius), is a common species in this group (Figure 30–81). The larvae feed on grape and Virginia creeper and sometimes defoliate them. There are larger forester moths in the Southwest. The black and yellow *Gerra sevorsa* (Grote) of Arizona resembles some arctiids.

Subfamily Amphipyrinae: This subfamily includes the genus *Spodoptera* (which contains several species of armyworms) and such colorful diurnal moths as the western species of *Annaphila*.

Subfamilies Noctuinae and Hadeninae: The larvae of many species in these groups (and in some other subfamilies as well) are called "cutworms" because they feed on the roots and shoots of various herbaceous plants, and often cut the plant off at the surface of the ground. The cutworms are nocturnal in habit and hide under stones or in the soil during the day. The most important cutworms belong to the genera *Agrotis, Euxoa, Feltia*, and *Peridroma* of the Noctuinae and to *Lacinipolia, Nephelodes*, and *Scotogramma* of the Hadeninae.

The corn earworm, *Helicoverpa zea* (Boddie) (Heliothinae), is a serious pest. The larva feeds on a number of plants, including corn, tomato, and cotton, and is sometimes called the "tomato fruitworm" or the "cotton bollworm." When feeding on corn (Figure 30–83), the larva enters the corn ear on the silks and eats the kernels from the tip of the cob. It burrows in tomato fruits

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Figure 30–83 Larva of the corn earworm, *Helicoverpa zea* (Boddie).

and into cotton bolls. The adults are light yellowish and vary somewhat in their markings (Figure 30–80G).

The armyworm, *Pseudaletia unipuncta* (Haworth) (Hadeninae), feeds on various grasses and frequently does serious damage to wheat and corn. The common name of this insect refers to the fact that the larvae frequently migrate in large numbers to a new feeding area. The moths are light brown with a single, white spot in the middle of each front wing (Figure 30–80H).

Family **Pantheidae**: This family differs from Noctuidae by lacking a countertympanal hood and in some larval characters. Nearly 25 species, mainly *Panthea* and *Raphia* occur in North America. The larvae feed mainly on woody plants.

Family **Lymantriidae—Tussock Moths and Their Relatives:** The lymantriids are medium-sized moths that are similar to the Noctuidae but differ in that they lack ocelli and have a larger basal areole in the hind wing (Figure 30–28). In most species (Figure 30–28A), M_1 in the hind wing is stalked with Rs for a short distance beyond the apex of the discal cell. The larvae are rather hairy and feed chiefly on trees. The tussock, gypsy, and browntail moths are serious pests of forest and shade trees. The tussock moths are native species, whereas the other two were introduced from Europe. There are 32 species of lymantriids in North America.

The white-marked tussock moth, *Orgyia leucostigma* (J. E. Smith) (Figure 30–84), is a common species throughout most of North America. The males are gray, with lighter hind wings and plumose antennae, and the females are wingless. The eggs are laid on tree trunks or branches, usually near the cocoon from which the female emerged, and the species overwinters in the egg stage. The larva (Figure 30–84A) can be recognized by the characteristic tufts or brushes of hairs.

The gypsy moth, *Lymantria dispar* (L.), was introduced from Europe into Massachusetts about 1866. Since then it has become widely distributed throughout New England and Mid-Atlantic states south to Virginia, as well as Ohio, Michigan, and Wisconsin and has caused widespread damage to forest trees. The females are white with black markings, and the males are gray (Figure 30–85). The females have a wingspread of about 40 to 50 mm, and the males are a little smaller. The eggs are laid on tree trunks or similar places, in a mass of the body hairs from the female. They overwin-

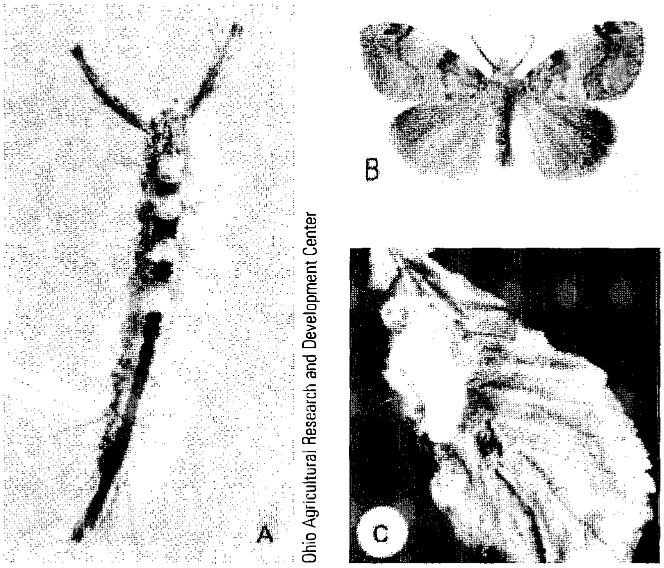

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Figure 30–84 The white-marked tussock moth, *Orgyia leucostigma* (Abbott and Smith). A, larva; B, adult male; C, adult female. Slightly enlarged.

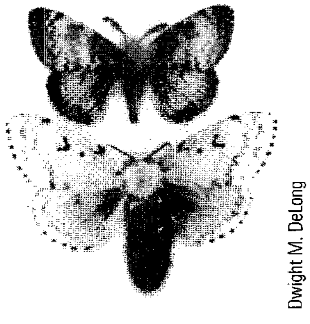

Figure 30–85 The gypsy moth, *Lymantria dispar* (L.), ⅓ ×. Male above, female below.

ter and hatch the following spring. The females are very weak fliers and seldom travel very far from the cocoon from which they emerge. The dispersal of the species is accomplished largely by the young larvae.

The browntail moth, *Euproctis chrysorrhoea* (L.), is another serious pest of forest and shade trees that was introduced from Europe. It first appeared near Boston in the early 1890s and has since spread throughout New England. The adults are white, with a wingspread of 25–35 mm, and they have brownish hairs at the end of the abdomen. The males are a little smaller than the females. This species passes the winter as a larva in a leaf shelter. Both sexes are winged. The hairs of the larva, when blown onto human skin, cause an irritating rash.

The satin moth, *Leucoma salicis* (L.), is a European species that appeared in the United States in 1920. It feeds on poplars and willows and is an occasional pest of poplars planted as shade trees or windbreaks. After its introduction it was considered an important pest, but the introduction of some European parasites has greatly reduced its numbers and importance.

***Family* Nolidae:** This group, which was formerly considered a subfamily of Noctuidae, contains small moths that have ridges and tufts of raised scales on the front wings. *Nola ovilla* Grote is fairly common in Pennsylvania on the trunks of beeches and oaks. The larva feeds on the lichens growing on the trunks of these trees. The larva of *N. triquetrana* (Fitch), a gray moth with a wingspread of 17–20 mm, feeds on apple, but it is seldom numerous enough to do much damage. The larva of the sorghum webworm, *N. sorghiella* Riley, is a pest of sorghum.

***Family* Arctiidae—Tiger Moths, Footmen Moths, Wasp Moths, and Others:** Kitching and Rawlins in Kristensen 1998 proposed a major rearrangement of this family that recognizes three subfamilies, of which only two are found in the United States and Canada. All are characterized by the presence of a pair of dorsal, eversible pheromone glands that are associated with the anal papillae of females. There are more than 260 species in North America.

Subfamily Lithosiinae—Footman Moths: The footman moths are small and slender, and most North American species are rather dull in color. Some tropical species, however, are very colorful. The larvae of most species feed on lichens. The striped footman moth, *Hypoprepia miniata* (Kirby), is a beautiful insect. It has pinkish front wings with three gray stripes, and the hind wings are yellow and broadly margined with gray. The lichen moth, *Lycomorpha pholus* (Drury), is a small, blackish moth with yellowish wing base (Figure 30–86C). It looks a little like some of the lycid beetles. These moths live in rocky places, and their larvae feed on lichens that grow on the rocks. Many species of the genus *Cisthene* are gray with various red markings or have other color combinations.

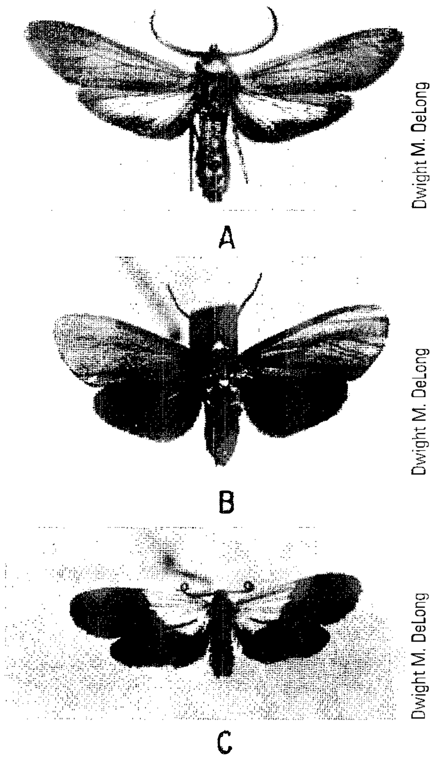

Figure 30–86 Arctiid moths. A, the yellow-collared scape moth, *Cisseps fulvicollis* (Hübner), 1½×; B, the Virginia ctenucha, *Ctenucha virginica* (Charpentier), natural size; C, the lichen moth, *Lycomorpha pholus* (Drury), 1½×.

Subfamily Arctiinae—Tiger Moths: This group contains the majority of the species in the family, and many are very common insects. A few are occasionally rather destructive to trees and shrubs. Many are very colorful and thus popular with collectors. They are broadly distributed in temperate and tropical regions.

Most tiger moths are of small to medium size, and brightly spotted or banded. Some are white or rather uniformly brownish. The wing venation is very similar to that in the Noctuidae, but Sc and Rs in the hind wing are usually fused to about the middle of the discal cell (Figure 30–26). These moths are principally nocturnal and, when at rest, hold the wings rooflike over the body. The larvae are usually hairy, sometimes very. The so-called woollybear caterpillars belong to this group. The cocoons are made largely from the body hairs of the larvae.

The tiger moths in the genera *Apantesis* and *Grammia* have black front wings with red or yellow stripes, and the hind wings are usually pinkish with black spots. One of the largest and most common species in the genus is *G. virgo* (L.), which has a wingspread of about 50 mm (Figure 30–87A). The larva feeds on pigweed and other weeds, and winters in the larval stage.

Estigmene acrea (Drury) is another common tiger moth. The adults are white, with numerous small, black spots on the wings, and the abdomen is pinkish with black spots (Figure 30–87B). The male's hind wings are yellowish. The larva feeds on numerous grasses and is sometimes called the "salt-marsh caterpillar."

One of the best-known woollybear caterpillars is the banded woollybear, *Pyrrharctia isabella* (J. E. Smith). This caterpillar is brown in the middle and black at each end, and the adult is yellowish brown with three rows of small black spots on the abdomen. These caterpillars are often seen scurrying across the roadways in the fall. They overwinter as larvae and pupate in the spring. The larva feeds on various weeds. The amount of black in the larva in the fall is thought by some to vary proportionately with the severity of the coming winter.

The larvae of some of the tiger moths feed on trees and shrubs and often do serious damage. The fall webworm, *Hyphantria cunea* (Drury), is a common species of this type. The larvae build large webs, often enclosing a limb of foliage, and feed within the web. These webs are common on many types of trees in late summer and fall. In North America this species is usually only a nuisance, but it has been introduced into Europe, where it has become a serious pest. The adults are usually white with a few dark spots and have a wingspread of about 25 mm. Some are all white, or they may have varying amounts of black spotting. The larvae of the hickory tussock moth, *Lophocampa caryae* (Harris) (Figure 30–88B), feed on hickory and other trees. The larva is somewhat similar to that of the tussock moths in the genus *Orgyia*. The adults (Figure 30–88A) are light brown with white spots on the wings.

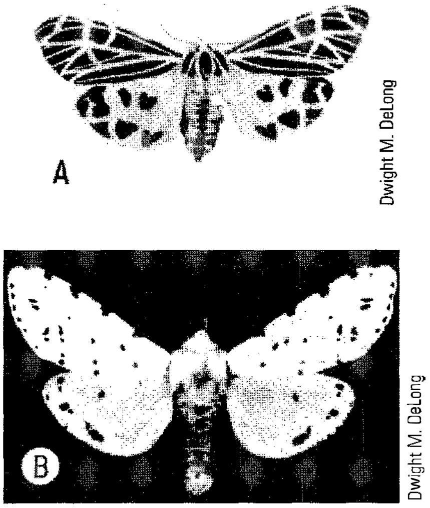

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Figure 30–87 Tiger moths (Arctiinae). A, the virgin tiger moth, *Grammia virgo* (L.), $^{3}/_{4}\times$; B, adult of the salt-marsh caterpillar, *Estigmene acrea* (Drury), $1^{1}/_{2}\times$.

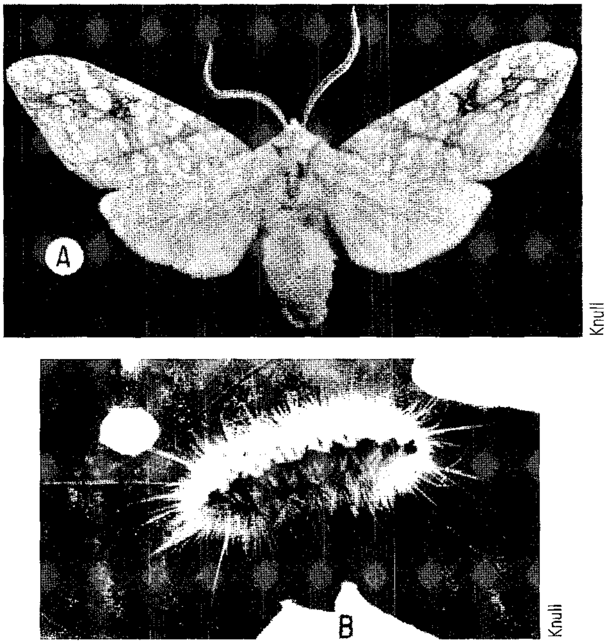

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Figure 30–88 The hickory tussock moth, *Lophocampa caryae* Harris (Arctiidae). A, adult, $1^{1}/_{2}\times$; B, larva.

Ctenuchas and wasp moths (tribe Ctenuchini) are small, day-flying moths, some of which are wasplike in appearance (but not as wasplike as the Sesiidae). Most species are tropical and very colorful. They can be recognized by the venation of the hind wing (Figure 30–25A): The subcosta is apparently absent. In the West, some species of ctenuchas are occasionally seen flying in large numbers, as if migrating.

Ctenucha virginica (Esper), a common species in the Northeast, has brownish black wings, a brilliant metallic bluish body, and an orange head (Figure 30–86B). The larva is a woolly, yellowish caterpillar that feeds on grasses. The cocoon is formed largely of the body hairs of the caterpillar. The yellow-collared scape moth, *Cisseps fulvicollis* (Hübner), is somewhat smaller than the ctenucha, with narrower wings and with the central portion of the hind wings lighter. Its prothorax is yellowish (Figure 30–86A). The larva of this species feeds on grasses, and the adults frequent goldenrod flowers.

Collecting and Preserving Lepidoptera

The order Lepidoptera contains many large and showy insects, and many students begin their collecting with these insects. Lepidoptera are generally fairly easy to collect, but they are more difficult to mount and preserve in good condition than insects in most other orders. Always handle specimens with great care, because the scales, which give the specimens their color, are easily rubbed off, and in many species the wings are easily torn or broken.

Lepidoptera can be collected with a net, or they can be gotten directly into a killing jar without the use of a net. A net for collecting these insects should be of a fairly light mesh, light enough that the specimen can be seen through the net. Once netted, a specimen should be placed into a killing jar or stunned as quickly as possible so it will not damage its wings by fluttering and attempting to escape. Many collectors prefer to insert the killing jar into the net to get the specimen into the jar without handling the specimen directly. The killing jar should be of sufficient toxic strength to stun the insect quickly. If the specimen is removed to the killing jar by hand, grasp it carefully through the net by the thorax, pinch it slightly to stun it, and then place it in the killing jar. Do not pinch delicate species such as blues and hairstreaks. Large moths are most easily killed by injecting alcohol into the thorax with a hypodermic needle (only a few drops are needed).

Many moths can be taken directly into a killing jar without using a net. Simply place a wide-mouthed jar over the specimen when it is resting on some flat surface. The killing agent in the jar should be strong enough to stun the insect quickly, before it can flutter about too much inside the jar and damage its wings.

Many species, particularly butterflies, frequent flowers and can be collected while feeding. To obtain a large number of species, visit a variety of habitats and collect at all seasons. Many species live only in certain habitats, and many have a short adult life and are on the wing only a short time each year.

Many moths are most easily collected at lights, especially ultraviolet ("black") and mercury vapor lights. They can be collected by traps, but specimens collected in this way are often in poor condition unless special precautions are taken. Traps should have a screen of ⅜-inch (1-cm) mesh near the bottom to keep large specimens away from smaller ones, and there should be plenty of folded paper and the like to provide hiding places. A strong poison is needed, such as cyanide, and thus considerable care is needed in operating the trap. A stun trap could be made by using blocks of ice in the bottom, with ample provision for keeping the moisture down. The low temperatures in such a trap would immobilize the specimens, which could be removed in the morning or after a few hours of operation.

Specimens can be collected at lights if there is a flat, white surface near the light for the insects to land on. The specimens can be taken directly from such a surface into a killing jar. Many interesting species can be obtained by sugaring (see Chapter 35).

Take precautions to prevent specimens from becoming damaged after they are placed in the killing jar. Don't place large, heavy-bodied specimens in a jar along with small, delicate ones. Don't let the jar become too crowded. Remove the specimens soon after they have been stunned, and then place them in paper envelopes. Small moths are perhaps best killed in small cyanide vials (such as shown in Figure 35–2A), with pieces of cleansing tissue inside to prevent the insects from touching each other too much.

The best way to obtain good specimens of many species is to rear them, from either larvae or pupae. Suggestions for rearing are given in Chapter 35. By rearing, the collector not only obtains good specimens, but also can become acquainted with the larval stages of different species and the plants on which the larvae feed.

Specimens of Lepidoptera can be preserved in a collection in two ways: in paper envelopes (as in the case of Odonata and some other groups), or spread and pinned. Use envelopes for temporary storage or in cases where the collection is large and space is not available for large numbers of spread specimens. To display your collection, the most useful type of mount is a glass-topped drawer. The best collections of Lepidoptera have the specimens pinned and spread. Many collectors find it best to pin the smaller moths in the field and to spread them later. Moths with a wingspread of less than 10 mm should generally be pinned with a minuten pin and double-mounted as shown in Figure 35–13D.

All Lepidoptera that are pinned or mounted under glass should be spread. The beginning student or the person interested principally in displaying his or her collection is advised to spread the specimens in an upside-down position (Figure 35–12). The advanced student or the person making a large collection should pin them or keep them in envelopes. Methods of spreading and mounting Lepidoptera are described in Chapter 35. It takes a little practice to become proficient in spreading these insects, and some of the smaller specimens will tax the skill and patience of the collector, but the resulting collection will be worth the effort. With the right equipment and practice, even microlepidoptera can be spread. Some collectors spread micros in the field, or at least "puff" out their wings, that is, blow on the specimens to lift and separate the wings.

In a large collection of pinned Lepidoptera, space can be saved by putting the pins into the bottom of the box at an angle and overlapping the wings of adjacent specimens. This is called *shingling*. A collection must be protected against museum pests by having naphthalene or some similar repellent in the boxes. Keep it in the dark, because many specimens fade if exposed to light for long periods.

References

Adamski, D., and R. L. Brown. 1989. Morphology and systematics of North American Blastobasidae (Lepidoptera: Gelechioidea). Mississippi Agric. and Forestry Exp. Sta. Tech. Bull. 165, 170 pp.

Allen, J. T. 1997. The Butterflies of West Virginia and Their Caterpillars. Pittsburgh: University of Pittsburgh Press, 224 pp.

Anonymous. 1972. An amateur's guide to the study of the genitalia of Lepidoptera. Hanworth: The Amateur Entomologist's Society. 16 p.

Bordelon, C., and E. Knudson. 1998. Checklist of Lepidoptera of the Audubon Palm Grove Sanctuary, Texas. Texas Lepidoptera Survey, Publ. 1. Houston: Knudson and Bordelon, 32 pp.

Bordelon, C., and E. Knudson. 1998. Checklist of Lepidoptera of the Big Thicket National Preserve, Texas. Texas Lepidoptera Survey, Publ. 2. Houston: Knudson and Bordelon, 42 pp.

Bordelon, C., and E. Knudson. 2002. Checklist of Butterflies of the Lower Rio Grande Valley, Texas. Texas Lepidoptera Survey, Publ. 9A. Houston: Knudson and Bordelon, 52 pp.

Braun, A. F. 1948. Elachistidae of North America (Microlepidoptera). Mem. Amer. Entomol. Soc. 13:1–110.

Braun, A. F. 1963. The genus *Bucculatrix* in America north of Mexico (Microlepidoptera). Mem. Amer. Entomol. Soc. 18:1–208.

Braun, A. F. 1972. Tischeriidae of America north of Mexico (Microlepidoptera). Mem. Amer. Entomol. Soc. 28:1–148.

Brewer, J. 1976. Butterflies. New York: Abrams, 176 pp.

Brown, F. M., D. Eff, and B. Rotger. 1957. Colorado Butterflies. Denver: Denver Museum of Natural History, 368 pp.

Bucheli, S., J.-F. Landry, and J. Wenzel. 2002. Larval case architecture and implications of host-plant associations for North American *Coleophora* (Lepidoptera: Coleophoridae). Cladistics 18:71–93.

Burns, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. Calif. Publ. Entomol. 37, 216 pp.

Capinera, J. L., and R. A. Schaefer. 1983. Field identification of adult cutworms, armyworms, and similar crop pests collected from light traps in Colorado. Fort Collins, CO: Cooperative Extension Service Colorado State University Bulletin 514A. 24 p.

Chapman, P. J., and S. E. Lienk. 1971. Tortricid Fauna of Apple in New York. Geneva: N.Y. State Agricultural Experiment Station, Cornell University, 122 pp.

Collins, M. M., and R. D. Weast. 1981. Wild Silk Moths of the United States: Saturniinae. Cedar Rapids, IA: Collins Radio Company, 138 pp.

Common, I. F. B. 1970. Lepidoptera (moths and butterflies). In CSIRO, The Insects of Australia, pp. 765–866. Melbourne: Melbourne University Press.

Common, I. F. B. 1975. Evolution and classification of the Lepidoptera. Annu. Rev. Entomol. 20: 183–203.

Common, I. F. B. 1990. Moths of Australia. Carlton, Victoria: Melbourne University Press, 535 pp.

Comstock, J. H. 1940. An introduction to entomology, 9th ed. Ithaca, NY: Comstock Publishing Company, Inc. 1064 pp.

Covell, C. V., Jr. 1984. A Field Guide to the Moths of Eastern North America. Boston: Houghton Mifflin, 496 pp.

Davis, D. R. 1964. Bagworm moths of the western Hemisphere (Lepidoptera: Psychidae). Bull. U.S. Natl. Mus. 244:1–233.

Davis, D. R. 1967. A revision of the moths of the subfamily Prodoxinae (Lepidoptera: Incurvariidae). Bull. U.S. Natl. Mus. 255:1–170.

Davis, D. R. 1968. A revision of the American moths of the family Carposinidae (Lepidoptera: Carposinoidea). Bull. U.S. Natl. Mus. 289:1–105.

Davis, D. R. 1975. A review of the Ochsenheimeriidae and the introduction of the cereal stem moth, *Ochsenheimeria vacculella* into the United States (Lepidoptera: Tineoidea). Smithson. Contrib. Zool. No. 192, 20 pp.

Davis, D. R. 1978a. A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae (Lepidoptera). Smithson. Contrib. Zool. No. 51, 131 pp.

Davis, D. R. 1978b. The North American moths of the genera *Phaeoses*, *Opogona*, and *Oinophila*, with a discussion of the supergeneric affinities (Lepidoptera: Tineidae). Smithson. Contrib. Zool. No. 282, 39 pp.

Davis, D. R., O. Pellmyr, and J. N. Thompson. 1992. Biology and systematics of *Greya* Busck and *Tetragma*, new genus (Lepidoptera: Prodoxidae). Smithson. Contrib. Zool. No. 524, 88 pp.

Davis, D. R., and G. Deschka. 2001. Biology and systematics of the North American *Phyllonorycter* leafminers on Salicaceae, with a synoptic catalog of the Palearctic species (Lepidoptera: Gracillariidae). Smithson. Contrib. Zool. 614:1–89.

Dominick, R. B. (Ed.). 1972. The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. (This ongoing series, when complete, will consist of identification manuals for all species of moths in North America north of Mexico. It will be published in about 150 parts, making 30 fascicles, written by selected specialists. The parts published to date are listed here under their respective authors.)

Dornfeld, F. J. 1980. The Butterflies of Oregon. Forest Grove: Timber Press, 275 pp.

Dos Passos, C. F. 1964. A synoptic list of Nearctic Rhopalocera. Lepidop. Soc. Mem. 1; 145 pp.

Duckworth, W. D. 1964. North American Stenomidae (Lepidoptera: Gelechioidea). Proc. U.S. Natl. Mus. 116:23–72.

Duckworth, W. D., and T. D. Eichlin. 1977. A classification of the Sesiidae of America north of Mexico. Occas. Pap. Ent. (Calif. Dept. Agr.) 26:1–54.

Duckworth, W. D., and T. D. Eichlin. 1978. The clearwing moths of California (Lepidoptera: Sesiidae). Occas. Pap. Ent. (Calif. Dept. Agr.) 27:1–80.

Ebner, J. A. 1970. The butterflies of Wisconsin. Milwaukee Public Museum Popular Science Handbook No. 12. Milwaukee: Public Museum, 205 pp.

Ehrlich, P. R. 1958. The comparative morphology, phylogeny, and higher classification of the butterflies (Lepidoptera: Papilionoidea). Univ. Kan. Sci. Bull. 39(8):305–370.

Ehrlich, P. R., and A. H. Ehrlich. 1961. How to Know the Butterflies. Dubuque, IA: William C Brown, 262 pp.

Eichlin, T. D., and H. B. Cunningham. 1978. The Plusiinae (Lepidoptera: Noctuidae) of America north of Mexico, emphasizing genitalic and larval morphology. USDA Tech. Bull. 1567, 122 pp.

Eichlin, T. D., and W. D. Duckworth. 1988. Sesioidea: Sesiidae. In R. B. Dominick (Ed.), The Moths of America north of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 5.1, 176 pp.

Emmel, T. C. 1975. Butterflies. New York: Knopf, 260 pp.

Emmel, T. C., and J. F. Emmel. 1973. The butterflies of southern California. Nat. Hist. Mus. Los Angeles County. Sci. Ser. 26:1–148.

Evans, W. H. 1951–1955. Catalogue of American Hesperiidae, 3 vols. London: British Museum (Natural History), 521 pp.

Ferguson, D. C. 1972a. Saturniidae: Citheroniinae and Hemileucinae in part. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 20, Part 2A, 153 pp.

Ferguson, D. C. 1972b. Bombycoidea: Saturniidae (conclusion: Hemileucinae in part, and Saturniinae). In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 20, Part 2B, 264 pp.

Ferguson, D. C. 1978. Noctuoidea: Lymantriidae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 22.2, 110 pp.

Ferguson, D. C. 1985a. Geometroidea: Geometridae (part), subfamily Geometrinae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 18(1), 131 pp.

Ferguson, D. C. 1985b. Contributions toward reclassification of the world genera of the tribe Arctiini. Part l: Introduction and a revision of the *Neoarctia-Grammia* group (Lepidoptera: Arctiidae; Arctiinae). Entomography 3:181–275.

Ferris, C. D,. and F. M. Brown (Eds.). 1980. Butterflies of the Rocky Mountain States. Norman: University of Oklahoma Press, 442 pp.

Field, W. D. 1940. A manual of the butterflies and skippers of Kansas. Bull. Univ. Kan. Biol. Ser., Bull. Dept. Entomol. 12:1–328.

Field, W. D. 1971. Butterflies of the genus *Vanessa* and of the resurrected genera *Basaris* and *Cynthia* (Lepidoptera: Nymphalidae). Smithson. Contrib. Zool. No. 84, 105 pp.

Fletcher, D. S. 1979. The Generic Names of the Moths of the World. Vol. 3: Geometroidea. London: British Museum (Natural History).

Fletcher, D. S., and I. W. B. Nye. 1982. The Generic Names of the Moths of the World. Vol. 4: Bombycoidea, Mimallonoidea, Sphingoidea, Castnioidea, Cossoidea, Zygaenoidea, Sesioidea. London: British Museum (Natural History).

Fletcher, D. S., and I. W. B. Nye. 1984. The Generic Names of the Moths of the World. Vol. 5: Pyraloidea. London: British Museum (Natural History).

Forbes, W. T. M. 1923–1960. Lepidoptera of New York and neighboring states. Part I: Primitive forms, Microlepidoptera. Cornell Univ. Agr. Expt. Sta. Mem. 68, 729 pp. (1923). Part 2: Geometridae, Sphingidae, Notodontidae, Lymantriidae. Cornell Univ. Agr. Expt. Sta. Mem. 274, 263 pp. (1948). Part 3: Noctuidae. Cornell Univ. Agr. Expt. Sta. Mem. 329, 433 pp. (1954). Part 4: Agaristidae through Nymphalidae including butterflies. Cornell Univ. Agr. Expt. Sta. Mem. 371, 188 pp. (1960).

Ford, E. B. 1944. Moths. London: Collins, 266 pp.

Franclemont, J. C. 1973. Mimallonoidea and Bombycoidea: Apatelodidae, Bombycidae, Lasiocampidae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 20, Part 1; 86 pp.

Freeman, H. A. 1969. Systematic review of the Megathymidae. J. Lepidop. Soc. 23 (Suppl. 1):1–59.

Garth, J. S., and J. W. Tilden. 1986. California Butterflies. Berkeley: University of California Press, 208 pp.

Handfield, L. 1999. Le guide des papillons du Quebec (version scientifique). Ottawa: Broquet, 982 pp.

Hardwick, D. F. 1965. The corn earworm complex. Mem. Entomol. Soc. Can. 40:1–245.

Hardwick, D. F. 1970a. A generic revision of the North American Heliothidinae (Lepidoptera: Noctuidae). Mem. Entomol. Soc. Can. 73:1–59.

Hardwick, D. F. 1970b. The genus *Euxoa* (Lepidoptera: Noctuidae) in North America. Part 1: Subgenera *Orosagrotis*, *Longivesica, Chorizagrotis, Pleonoctopoda,* and *Crassivesica.* Mem. Entomol. Soc. Canada 67:1–177.

Hardwick, D. F. 1996. A monograph to the North American Heliothentinae (Lepidoptera: Noctuidae). Ottawa: D. F. Hardwick, 281 pp.

Harris, L., Jr. 1972. Butterflies of Georgia. Norman: University of Oklahoma Press, 326 pp.

Hasbrouck, F. F. 1964. Moths of the family Acrolophidae in America north of Mexico (Microlepidoptera). Proc. U.S. Natl. Mus. 114:487–706.

Heinrich, C. 1923. Revision of the North American moths of the subfamily Eucosminae of the family Olethreutidae. Bull. U.S. Natl. Mus. 123:1–298.

Heinrich, C. 1926. Revision of the North American moths of the subfamilies Laspyresiinae and Olethreutinae. Bull. U.S. Natl. Mus. Bull. 132:1–261.

Heinrich, C. 1956. American moths of the subfamily Phycitinae. Bull. U.S. Natl. Mus. 207:1–581.

Heppner, J. B. 1985. The Sedge Moths of North America (Lepidoptera: Glyphipterigidae). Gainesville, FL: Flora and Fauna, 254 pp.

Heppner, J. B. 1991. Faunal regions and the diversity of Lepidoptera. Tropical Lepidoptera 2 (Suppl. 1), 85 pp.

Heppner, J. B. 1998. Classification of Lepidoptera. Part 1: Introduction. Holarctic Lepidoptera, 5 (Suppl. 1), 1148 pp.

Heppner, J. B., and W. D. Duckworth. 1981. Classification of the superfamily Sesioidea (Lepidoptera: Ditrysia). Smithson. Contrib. Zool. 314:1–144.

Hodges, R. W. 1962. A revision of the Cosmopterigidae of America north of Mexico, with a definition of the Momphidae and Walshiidae (Lepidoptera). Entomol. Amer. 42:1–171.

Hodges, R. W. 1964. A review of the North American moths in the family Walshiidae (Lepidoptera: Gelechioidea). Proc. U.S. Natl. Mus. 115:289–330.

Hodges, R. W. 1966. Revision of the nearctic Gelechiidae. Part 1: The *Lita* group (Lepidoptera: Gelechioidea). Proc. U.S. Natl. Mus. 119:1–66.

Hodges, R. W. 1971. Sphingoidea: Sphingidae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 21. 158 pp.

Hodges, R. W. 1974. Gelechioidea, Oecophoridae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 6.2. 142 pp.

Hodges, R. W. 1978. Gelechioidea, Cosmopterigidae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 6.1. 166 pp.

Hodges, R. W. 1986. Gelechioidea: Gelechiidae (part), Dichomeridinae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 7.1. 178 pp.

Hodges, R. W. 1999. Gelechioidea: Gelechiidae (part Chionodes). In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 7.6. 348 pp.

Hodges, R. W., et al. 1983. Check List of the Lepidoptera of America North of Mexico. London: E. W. Classey and Wedge Entomolological Research Foundation, 284 pp.

Holland, W. J. 1931. The Butterfly Book, rev. ed. New York: Doubleday, 424 pp.

Holland, W. J. 1968. The Moth Book. New York: Dover, 479 pp. (First published in 1903)

Holloway, J. D., J. D. Bradley, and D. J. Carter. 1987. CIE Guides to Insects of Importance to Man. 1. Lepidoptera. Wallingford: CAB International. 262 p.

Hooper, R. R. 1973. The Butterflies of Saskatchewan. Regina, Canada: Museum of Natural History, 216 pp.

Howe, W. H. (Ed.). 1975. The Butterflies of North America. New York: Doubleday, 632 pp.

Kaila, L. 1995. A review of *Coelopoeta* (Elachistidae), with descriptions of two new species. J. Lepidop. Soc. 49:171–178 .

Kaila, L. 1996. Revision of the Nearctic species of *Elachista.* Part 1: The *tetragonella* group (Lepidoptera: Elachistidae). Entomol. Scand. 227:217–238.

Kaila, L. 1997. Revision of the Nearctic species of *Elachista s.l.* The *argentella* group (Lepidoptera: Elachistidae). Acta Zool. Fennica 206, 93 pp.

Kaila, L. 1999. Revision of the Nearctic species of *Elachista s.l.* Part 3: The *bifasciella, praelineata, saccharella,* and *freyerella* groups (Lepidoptera: Elachistidae). Acta Zool. Fennica 211, 235 pp.

Kimball, C. P. 1965. Lepidoptera of Florida. Arthropods of Florida and Neighboring Land Areas 1, 363 pp.

Klots, A. B. 1951. A Field Guide to the Butterflies. Boston: Houghton Mifflin, 349 pp.

Klots, A. B. 1958. The World of Butterflies and Moths. New York: McGraw-Hill, 207 pp.

Knudson, E., and C. Bordelon. 1999. Checklist of Lepidoptera of Big Bend National Park, Texas. Texas Lepidoptera Survey, Publ. 3. Houston: Knudson and Bordelon, 64 pp.

Knudson, E., and C. Bordelon. 2000. Checklist of Lepidoptera of Guadalupe Mts. National Park, Texas. Texas Lepidoptera Survey, Publ. 4. Houston: Knudson and Bordelon, 67 pp.

Knudson, E., and C. Bordelon. 2000. Checklist of Lepidoptera of the Caprock Canyonlands, Texas. Texas Lepidoptera Survey, Publ. 5. Houston: Knudson and Bordelon, 51 pp.

Knudson, E., and C. Bordelon. 2000. Checklist of the Lepidoptera of Texas (parts 1 & 2). Texas Lepidoptera Survey, Publ. 6. Houston: Knudson and Bordelon, 50 pp.

Knudson, E., and C. Bordelon. 2001. Checklist of Lepidoptera of the Davis Mountains, Texas. Texas Lepidoptera Survey, Publ. 7. Houston: Knudson and Bordelon, 48 pp.

Knudson, E., and C. Bordelon. 2001. Checklist of the Lepidoptera of the Texas Hill Country. Texas Lepidoptera Survey, Publ. 8. Houston: Knudson and Bordelon, 72 pp.

Knudson, E., and C. Bordelon. 2002. Texas Lepidoptera Atlas. Vol. 7: Sesioidea. Houston: Knudson and Bordelon, 32 pp.

Kristensen, N. P. (Ed.). 1998. Handbuch der Zoologie 4 (Arthropoda), (2) (Insecta), (35) (Lepidoptera. Moths and butterflies 1 Evolution, systematics and biogeography). Berlin: de Gruyter, 494 pp.

Lafontaine, J. D. 1987. Noctuoidea: Noctuidae, Noctuinae (part: *Euxoa*). In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 27.2, 234 pp.

Lafontaine, J. D. 1998. Noctuoidea: Noctuidae, (part Noctuinae). In R. B. Dominick (Ed.), The Moths of America north of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 27.3, 348 pp.

Lafontaine, J. D., and R. W. Poole. 1991. Noctuoidea: Noctuidae, (part Plusiini). In R. B. Dominick (Ed.), The Moths of America north of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 25.1, 182 pp.

Landry, B. 1995. A phylogenetic analysis of the major lineages of the Crambinae and of the genera of Crambini of North America (Lepidoptera:Pyralidae). Mem. Entomol.:242.

Landry, J.-F. 1991. Systematics of nearctic Scythrididae (Lepidoptera:Gelechioidea): phylogeny and classification of supraspecific taxa, with a review of described species. Mem. Entomol. Soc. Can. 160:1–341.

Layberry, R. L., P. W. Hall, and J. D. Lafontaine. 1998. The Butterflies of Canada. Toronto: University of Toronto Press, 280 pp.

MacKay, M. R. 1959. Larvae of North American Olethreutidae (Lepidoptera). Can. Entomol. Suppl. 10, 338 pp.

MacKay, M. R. 1968. The North American Aegeriidae (Lepidoptera): A revision based on late-instar larvae. Mem. Entomol. Soc. Can. 58:1–112.

MacKay, M. R. 1977. Larvae of the North American Tortricinae (Lepidoptera: Tortricidae). Can. Entomol. Suppl. 28, 182 pp.

MacNeill, C. D. 1964. The skippers of the genus *Hesperia* in western North America, with special reference to California (Lepidoptera: Hesperiidae). Univ. Calif. Publ. Entomol. 35:1–230.

McCabe, T. L. 1991. Atlas of Adirondack caterpillars with a host list, rearing notes and a selected bibliography of works depicting caterpillars. N.Y. State Mus. Bull. 470. 113 pp.

McDunnough, J. 1938–1939. Check list of the Lepidoptera of Canada and the United States of America. So. Calif. Acad. Sci. Mem. Part 1: Macrolepidoptera, 274 pp. (1938). Part 2: Microlepidoptera, 171 pp. (1939).

McGuffin, W. C. 1967–1981. Guide to the Geometridae of Canada (Lepidoptera). Mem. Entomol. Soc. Can. 50:1–67 (1967), 86:1–159 (1970), 101:1–191 (1977), 117:1–153 (1981).

Miller, J. C., and P. C. Hammond. 2000. Macromoths of northwest forests and woodlands. (USDA, Forest Service), Forest Health Technology Enterprise Team (FHTET)-98-18. Morgantown, WV, 133 pp.

Miller, L. D., and F. M. Brown. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Mem. Lepidop. Soc. 2:1–280.

Miller, W. E. 1987. Guide to the olethreutine moths of midland North America (Tortricidae). USDA For. Serv. Agr. Handbook 660. Washington, DC, 104 pp.

Morris, R. F. 1980. Butterflies and moths of Newfoundland and Labrador: The Macrolepidoptera. St. Johns: Agric. Can. Publ. 1691. 407 pp.

Mosher, E. 1916. A classification of the Lepidoptera based on characters of the pupa. Bull. Ill. State Lab. Nat. Hist. 12(2):17–159.

Munroe, E. G. 1972a. Pyralidae: Scopariinae and Nymphulinae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 13, Part 1A, 134 pp.

Munroe, E. G. 1972b. Pyralidae: Odontiinae and Glaphyriinae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 13, Part 1B, 125 pp.

Munroe, E. G. 1973. Pyralidae: The subfamily Evergestinae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 13, Part 1C, 51 pp.

Munroe, E. G. 1976a. Pyralidae: Pyraustinae. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 13, Part 2A, 78 pp.

Munroe, E. G. 1976b. Pyralidae: Pyraustinae, Tribe Pyraustini. In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 13, Part 2B, 69 pp.

Neunzig, H. H. 1986. Pyraloidea: Pyralidae (part), Phycitinae (part—*Acrobasis* and allies). In R. B. Dominick (Ed.), The Moths of America North of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 15.2, 82 pp.

Neunzig, H. H. 1990. Pyraloidea: Pyralidae, Phycitinae (part). In R. B. Dominick (Ed.), The Moths of America north of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 15.3, 165 pp.

Neunzig, H. H. 1997. Pyraloidea: Pyralidae, Phycitinae (part). In R. B. Dominick (Ed.), The Moths of America north of Mexico. Washington, DC: Wedge Entomological Research Foundation. Fasc. 15.4, 157 pp.

Newton, P. J., and C. Wilkinson. 1982. A taxonomic revision of the North American species of *Stigmella* (Lepidoptera: Nepticulidae). Syst. Entomol. 7:367–463.

Nielsen, M. C. 1999. Michigan Butterflies and Skippers. East Lansing, MI: Michigan State Univ. Ext. Bull., 248 pp.

Nye, I. W. B. 1975. The Generic Names of the Moths of the World. Vol. 1: Noctuoidea (part). London: British Museum (Natural History), 568 pp.

Nye, I. W. B., and D. S. Fletcher. 1986. The Generic Names of the Moths of the World. Vol. 6: Microlepidoptera. London: British Museum (Natural History), 368 pp.

Opler, P. A. 1992. A Field Guide to Eastern Butterflies. Boston: Houghton Mifflin, 396 pp.

Opler, P. A. 1999. A Field Guide to Western Butterflies, 2nd ed. Boston: Houghton Mifflin, 540 pp.

Opler, P. A., and G. O. Krizek. 1984. Butterflies East of the Great Plains: An Illustrated Natural History. Baltimore: Johns Hopkins University Press, 294 pp.

Parenti, U. 2000. A guide to the Microlepidoptera of Europe. Torino: Museo Regionale di Scienze Naturali. 426 p.

Peterson, A. 1948. Larvae of Insects. Part 1: Lepidoptera and Plant-Infesting Hymenoptera. Ann Arbor, MI: J. E. Edwards, 315 pp.

Pogue, M. G. 2002. A world revision of the genus *Spodoptera* Guenée (Lepidoptera: Noctuidae). Mem Amer. Entomol. Soc. 43:1–202.

Poole, R. W. 1989. Noctuidae. In J. B. Heppner (Ed.), Lepidopterorum Catalogus (new series). New York: E. J. Brill/ Flora and Fauna Publications. Fasc. 118, 1314 pp.

Poole, R. W. 1995. Noctuoidea: Noctuidae, Cucullinae, Stiriinae, Psaphidinae (part). In R. B. Dominick (Ed.), The Moths of America north of Mexico. Washington, DC:

Wedge Entomological Research Foundation. Fasc. 26.1, 249 pp.

Powell, J. A. 1964. Biological and taxonomic studies on tortricine moths, with reference to the species in California. Univ. Calif. Publ. Entomol. 32:1–317.

Powell, J. A. 1973. A systematic monograph of New World ethmiid moths (Lepidoptera: Gelechioidea). Smithson. Contrib. Zool. No. 120, 302 pp.

Powell, J. A., and W. G. Miller. 1978. Nearctic pine tip moths of the genus *Rhyacionia*; biosystematic review (Lepidoptera: Tortricidae, Olethreutinae). USDA For. Serv. Agr. Handbook 514:1–51.

Powell, J. A., and D. Povolny. 2001. Gnorimoschemine moths of coastal dune and scrub habitats in California (Lepidoptera: Gelechiidae). Holarctic Lepidoptera 8 (Suppl. 1), 53 pp.

Pyle, R. M. 2002. The Butterflies of Cascadia. Seattle: Seattle Audubon Society, 420 pp.

Rings, R. W. 1977. A pictorial key to the armyworms and cutworms attacking vegetables in the north central states. Ohio Agr. Res. Develop. Center, Res. Circ. 231, 36 pp.

Rings, R. W. 1977. An illustrated key to common cutworm, armyworm, and looper moths in the north central states. Ohio Agr. Res. Develop. Center, Res. Circ. 227, 60 pp.

Rings, R. W., E. H. Metzler, F. J. Arnold, and D. H. Harris. 1992. The owlet moths of Ohio, order Lepidoptera, family Noctuidae. Bull. Ohio Biol. Surv.(n.s.), 9(2), 219 pp.

Robinson, G. S., P. R. Ackery, I. J. Kitching, G. W. Beccaloni, and L. M. Hernández. 2002. Hostplants of the moth and butterfly caterpillars of America north of Mexico. Mem. Amer. Entomol. Inst. 69. 824 p.

Rockburne, E. W., and J. D. Lafontaine. 1976. The cutworm moths of Ontario and Quebec. Can. Dept. Agr. Publ. 1593, 164 pp.

Sargent, T. D. 1976. Legion of Night: The Underwing Moths. Amherst: University of Massachusetts Press, 222 pp.

Scoble, M. J. 1992. The Lepidoptera: Form, Function, and Diversity. Oxford, UK: Oxford University Press, 404 pp.

Scott, J. A. 1986. The Butterflies of North America. Stanford, CA: Stanford University Press, 583 pp.

Selman, C. L. 1975. A pictorial key to the hawkmoths (Lepidoptera: Sphingidae) of eastern United States (except Florida). Ohio Biol. Surv., Biol. Notes No. 9, 21 pp.

Shaffer, J. C. 1968. A revision of the Peoriinae and Anerastiinae (auctorum) of America north of Mexico (Lepidoptera: Pyralidae). Bull. U.S. Natl. Mus. 280:1–124.

Shull, E. M. 1987. The Butterflies of Indiana. Bloomington: Indiana University Press, 272 pp.

Solis, M. A. 1993. A phylogenetic analysis and reclassification of the genera of the *Pococera* complex (Lepidoptera: Pyralidae: Epipaschiinae). J. N.Y. Entomol. Soc. 101:1–83.

Stehr, F. W. (Ed.). 1987. Immature Insects. Dubuque, IA: Kendall/Hunt, 754 pp.

Stehr, F. W., and E. F. Cook. 1968. A revision of the genus *Malacosoma* Hübner in North America (Lepidoptera: Lasiocampidae): Systematics, biology, immatures, and parasites. Bull. U.S. Natl. Mus. 276:1–321.

Tietz, H. M. 1973. An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada, 2 vols. Sarasota, FL: A.C. Allyn, 1042 pp.

Tilden, J. W. 1965. Butterflies of the San Francisco Bay Region. Berkeley: University of California Press, 88 pp.

Tilden, J. W., and A. C. Smith. 1986. A Field Guide to Western Butterflies. Boston: Houghton Mifflin, 370 pp.

Tuskes, P. M., J. P. Tuttle, and M. C. Collins. 1996. The wild silk moths of North America: A natural history of the Saturniidae of the United States and Canada. Ithaca, NY: Cornell University Press, 250 pp.

Tyler, H. A. 1975. The Swallowtail Butterflies of North America. Healdsburg, CA: Naturegraph, 192 pp.

Urquhart, F. A. 1960. The Monarch Butterfly. Toronto: University of Toronto Press, 361 pp.

Villiard, P. 1969. Moths and How to Rear Them. New York: Funk and Wagnalls. 242 pp. (Reprinted by Dover.)

Wagner, D. L., D. C. Ferguson, T. L. McCabe, and R. C. Reardon. 2001. Geometroid caterpillars of Northestern and Appalachian forests. (USDA Forest Service) Forest Health Technology Enterprise Team (FHTET)-2001-10: 1–239.

Wagner, D. L., V. Giles, R. C. Reardon, and M. L. McManus. 1998. Caterpillars of eastern forests. USFS Technology Transfer Bull. FHTET-96-34:1–113.

Watson, A., D. S. Fletcher, and I. W. B. Nye. 1980. The Generic Names of the Moths of the World. Vol. 2: Noctuoidea (part). London: British Museum (Natural History), 228 pp.

Watson, A., and P. E. S. Walley. 1975. The Dictionary of Butterflies and Moths in Color. New York: McGraw-Hill, 296 pp.

Wilkinson, C. 1979. A taxonomic study of the microlepidopteran genera *Microcalyptris* Braun and *Fomoria* Beirne occurring in the United States of America (Lepidoptera: Nepticulidae). Tijds. Entomol. 122:59–90.

Wilkinson, C., and P. J. Newton. 1981. The microlepidopteran genus *Ectoedemia* Busck (Nepticulidae) in North America. Tijds. Entomol. 124:27–92.

Wilkinson, C., and M. J. Scobie. 1979. The Nepticulidae (Lepidoptera) of Canada. Mem. Entomol. Soc. Can. 107:1–129.

Winter, W. D., Jr. 2000. Basic techniques for observing and studying moths & butterflies. Mem. Lepidop. Soc. 5:1–444.

Zimmerman, E. C. 1958a. Insects of Hawaii. Vol. 7: Macrolepidoptera. Honolulu: University of Hawaii Press, 542 pp.

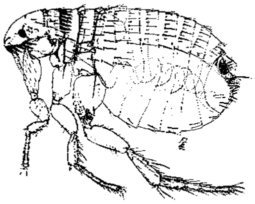
Zimmerman, E. C. 1958b. Insects of Hawaii. Vol. 8: Pyraloidea. Honolulu: University of Hawaii Press, 456 pp.

Zimmerman, E. C. 1978. Insects of Hawaii. Vol. 9: Microlepidoptera (2 parts). Honolulu: University of Hawaii Press, 1903 pp.

31

Order Siphonaptera[1,2]

Fleas



Fleas are small, wingless, holometabolous insects. With rare exception, the adults depend for nourishment on the blood of warm-blooded vertebrates. However, the larvae are relatively free-living and feed on organic material in the larval habitat. The bodies of adult fleas (Figure 31–1) tend to be laterally compressed and usually have caudally directed setae and spines that expedite forward progress through the vestiture of the host while resisting the backward movements frequently associated with the grooming activities of the host. Adults have shiny, hairy bodies and range from light, yellowish brown to almost black.

The adult head capsule may be "fracticipit," with a complete transverse interantennal groove connecting the antennal fossae dorsally, or "integricipit," in which the interantennal groove is absent. It usually bears a single frontal tubercle (Figure 31–2A) mesally on the frontal margin and a variable number of preantennal setal rows. A pair of eyes may be present, vestigial, or absent, but when present they arise along the dorsocephalic margin of an oblique linear depression containing the antennae, called the *antennal fossa.* In some groups the dorsal ends of these fossae are fused internally to form an oval or circular *trabecula centralis* or *area communis* (Figure 31–2A). The dorsal margin of the antennal fossae usually has a number of small setulae along at least part of its length. The genal lobe extends below and behind the eye and may bear a comb of two or more spines (Figure 31–1), or lack a comb altogether (Figure 31–2A). The postocular portion of the head capsule usually bears one or more rows of preoccipital setae cephalad of the occipital row. The antennae consist of a basal scape, a pedicel, and a nine-segmented flagellum, or clavus. Some of the segments may be at least partly fused, especially in the females of some species. In males, the mesal surface of the clavus usually bears a number of T-shaped holding organs that the male uses to engage with the female's basal abdominal sternite during copulation. The feeding apparatus includes a vestigial clypeus and mandibles and paired, usually four-segmented maxillary palpi arising on a triangular maxillary lobe. The labium usually has a 2- to 5-segmented labial palpus, although as many as 10 segments are known from species of *Chaetopsylla* (*Arctopsylla*), and as many as 20 in an extralimital genus belonging to the same family. The feeding fascicle consists of an unpaired epipharyngeal stylet and a pair of maxillary stylets derived from the laciniae, held together by the labial palpi. According to Snodgrass (1946), this condition is unique to the order, because other insects with piercing-sucking mouthparts have maxillary stylets derived from the galeae.

The thorax (Figure 31–2) consists of three distinct and somewhat separate segments. The pronotum is well demarcated and may have one to three rows of setae and frequently a distinct comb along its caudal margin. The propleurites and prosternum have lost their individual identities and form a composite, L-shaped structure, called the *prosternosome,* that is devoid of setae. The mesonotum and mesopleurites are well developed, but because of the lateral compression of the body, the mesosternum is much narrowed and reduced. The mesonotum may bear a number of regular or irregular rows of setae and there may be a number of pseudosetae along the internal caudal margin of the mesonotal collar (Figure 31–2). The pleural sclerites

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[1] Siphonaptera: *siphon*, a tube; *aptera*, wingless.

[2] We are indebted to Dr. Robert E. Lewis for most of the material in this chapter.

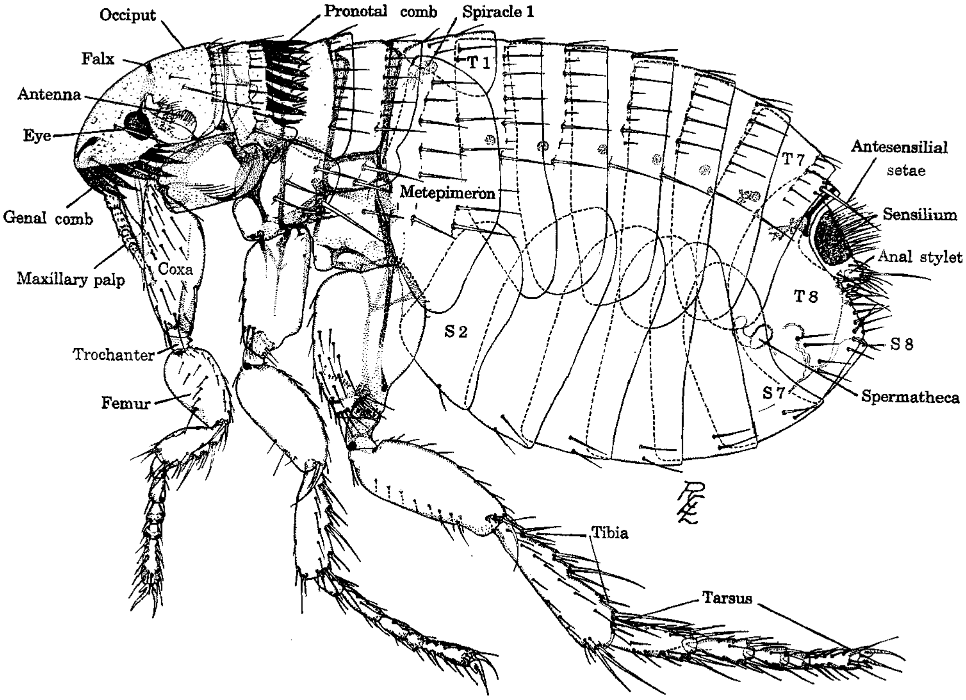


Figure 31–1 An adult cat flea, *Ctenocephalides felis* (Bouché) (Pulicidae, Archaeopsyllinae). (Figure prepared by Robert E. Lewis.)

are divided into an anterior mesepisternum and a posterior mesepimeron by a subvertical pleural rod. The caudal margin of the latter is articulated with the following segment by a lateral link plate arising above the spiracle. The metathorax also is well developed, with a distinct metanotum and large, shield-shaped metapleurites. The metanotum bears a smaller ventral, lobe-shaped lateral metanotal area and the upper portion may have a variable number of regular or irregular setal rows and a few small spinelets on the caudal margin. The metapleurites usually are divided by a large, subvertical pleural rod, the dorsal end expanded to form a cup-shaped "ball and socket" joint with the metanotum that usually is lined with resilin, a colorless, rubberlike, elastic protein best developed in those species that are good jumpers. The anterior metepisternum usually is relatively devoid of setae, but the posterior metepimeron bears a spiracle and a number of long setae, the arrangement of which is sometimes useful in identification.

The legs of most adult fleas are similar in form and function, allowing the individual to progress by walking or jumping. Exceptions include species that attach themselves more or less permanently to their hosts and those that are restricted to the nest or lair of their hosts. In the former instance, all or part of a leg may be permanently lost, whereas in the latter the individual moves by simply crawling. In typical adults the leg consists of a large, flattened coxa, a small trochanter, flattened femur and tibia, and a 5-segmented tarsus, the terminal segment of which bears three to five pairs of lateral plantar setae and an apical pair of claws called ***ungues*** (Figure 31–1). The configuration of the ungues is evidently determined by the nature of the host's pelage.

The abdomen of adult fleas consists of eight distinct segments plus a compound terminal area in which segmentation is indistinct. Tergum 1 is small and unmodified, but may bear a few small spinelets on its caudal margin. Abdominal sternite 1 is vestigial in both sexes. As a result, the first visible sternite is number 2. Tergites and sternites 2 to 7 are unmodified. The tergites may have a variable number of setal rows and at least the anteriormost segments also may bear marginal spinelets. The sternites usually only have a single row of setae, situated in the ventral half of each segment. The remaining abdominal segments are variously modified to form the internal and external genitalia. The caudal margin of tergum 7 in both sexes usually has a variable number of antesensilial setae. Tergum 8 bears a large, spiracular fossa cephalad of the

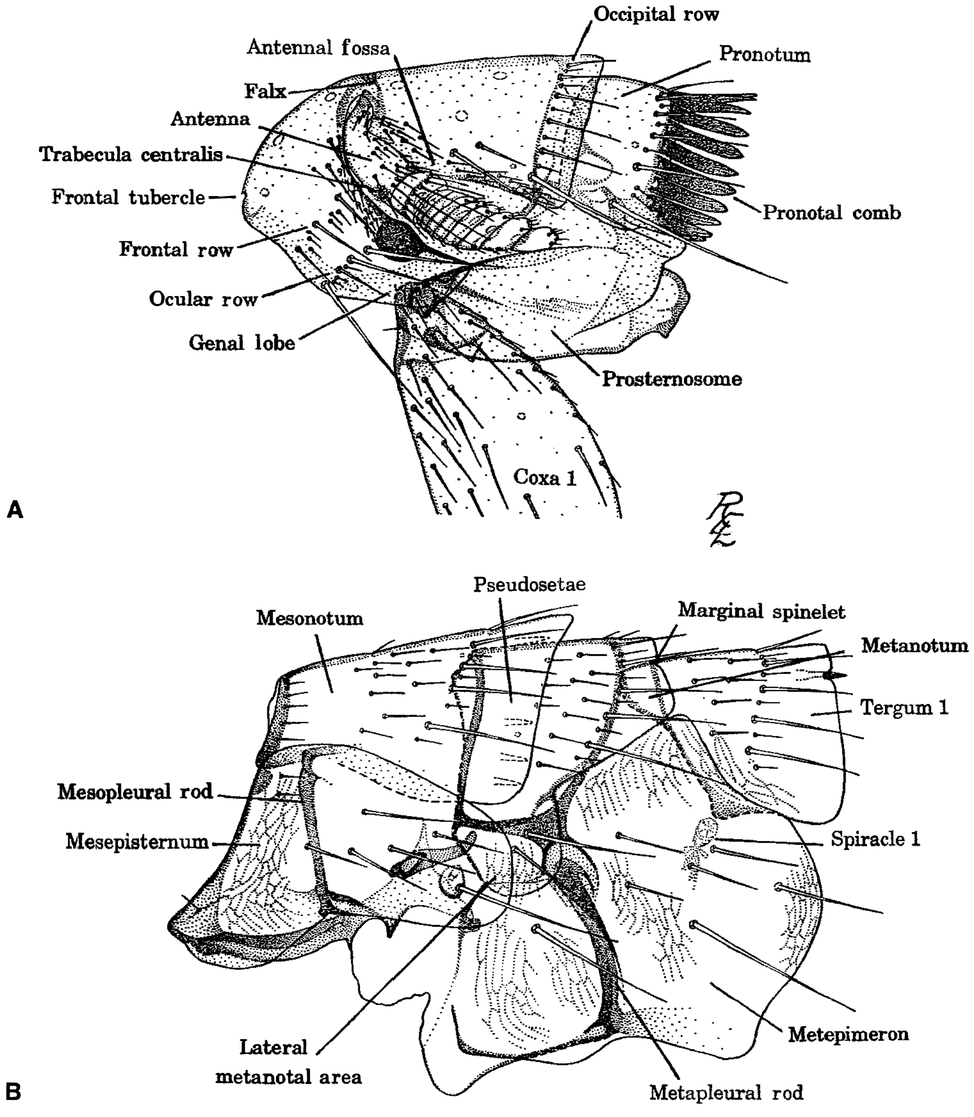


Figure 31–2 *Smitipsylla maseri* Lewis (an extralimital species), showing structures of taxonomic importance. A, head and prothorax of male; B, mesothorax and metathorax of male. (Figure prepared by Robert E. Lewis.)

circular to oval sensilium, which may be convex, flat, or slightly concave, depending on the family. In females these modified segments contribute to the anal lobes, anal stylets, genital ducts and spermathecae. In males, tergites 9 to 11 contribute to the anal lobes and claspers, whereas sternites 9 to 10 contribute to the ventral sternal appendages if they are present. Different entomologists have variously interpreted the homologies of the aedeagus (for example, Traub 1950, Peus 1956, Smit 1970), but further study is required before the structure and function of this complicated structure are understood across the various families.

Taxonomic Characters

As indicated elsewhere, identification of adult fleas at the species level usually involves analysis of genitalia, especially those of the males (Figure 31–3A,B). In many genera the identity of females can only be inferred from the identification of accompanying males. However, a number of nongenitalic characters are useful for identification at the generic level. Most are mentioned in the introductory section and need not be discussed further. However, the genitalic structures are much more complicated and require further explanation.

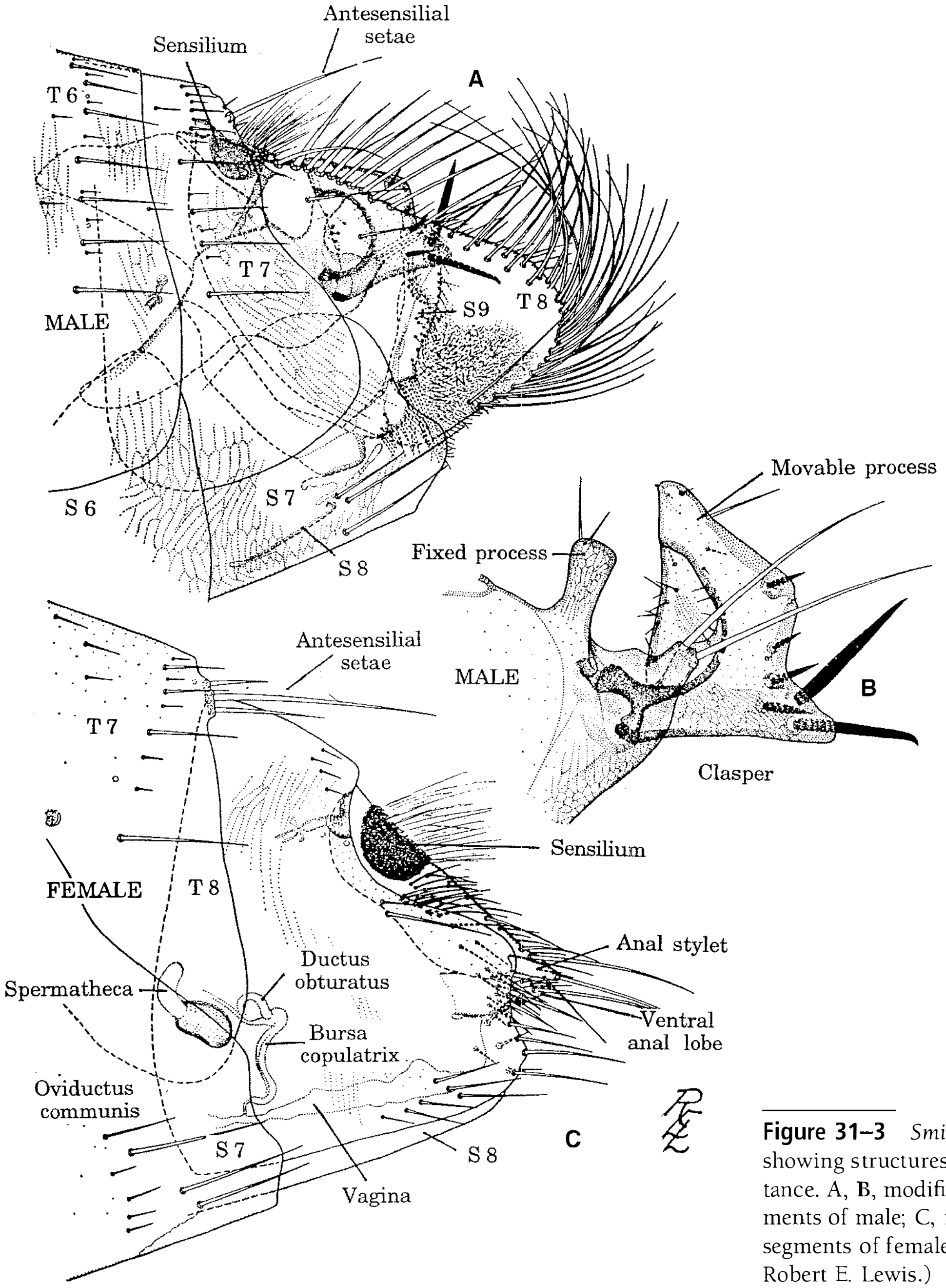


Figure 31–3 *Smitipsylla maseri* Lewis, showing structures of taxonomic importance. A, B, modified abdominal segments of male; C, modified abdominal segments of female. (Figure prepared by Robert E. Lewis.)

Very few features of the female anatomy are useful in identification. Beyond the usual somatic characters, they are found in the abdominal segments 7 to 11 (Figure 31–3C). Externally these include the number of antesensilial setae, the shape of the anal stylet and dorsal anal lobes, the form of the caudal margin of sternite 7 and the setation of tergite and sternite 8. Useful internal structures, at least in some species, include the form of the spermatheca(e) and the shape and degree of sclerotization of the genital ducts.

In males the aedeagus is a complicated structure consisting of a number of parts of uncertain function, as well as the penis rods, the functional intromittent organ. Although the families vary considerably with respect to the other genitalic characters, the following is a general description among the families under consideration. Tergites 9 to 10 are modified into paired clasping organs (Figure 31–3B), the fixed and movable processes. The former are derived from the dorsal portion of the ventral, handlelike extension of the body of the clasper, the manubrium. The latter are articulated with the caudal margin of the manubrium. Sternites 8 to 9 are appendiculate and may be adorned with a variety of appendages or other modifications. The apex of the aedeagus also may have various anchoring mechanisms that ensure the integrity of the union between the male and female genitalia during coitus. Among the North American families, one or more of these modified segments may be reduced or even absent.

Taxonomic characters in the larvae include form of the mouthparts; shape of the egg burster on the dorsum of the head capsule (shed with the first-instar exuvia); shape of the antennae and antennal mound and its sensory structures; and chaetotaxy of the head capsule, thorax, and abdominal segments. Although legs are absent, the terminal abdominal segment is provided with a pair of anal struts that may be used to grasp fibers in the host's nest. By engaging the substratum with the mouthparts and pushing with the anal struts, larvae can move forward rather rapidly.

Classification of the Siphonaptera

Superfamily Ceratophylloidea
  Ceratophyllidae
    Ceratophyllinae (112): *Aetheca* (2), *Amalaraeus* (2), *Amaradix* (3), *Amonopsyllus* (1), *Amphalius* (1), *Ceratophyllus* (22), *Dasypsyllus* (2), *Eumolpianus* (7), *Jellisonia* (2), *Malaraeus* (3), *Margopsylla* (1), *Megabothris* (8), *Mioctenopsylla* (2), *Monopsyllus* (1), *Nosopsyllus* (2), *Opisodasys* (6), *Orchopeas* (15), *Oropsylla* (13), *Pleochaetis* (1), *Plusaetis* (2), *Psittopsylla* (1), *Rosickyiana* (1), *Tarsopsylla* (1), *Thrassis* (11), *Traubella* (2)
    Dactylopsyllinae (15): *Dactylopsylla* (7), *Foxella* (1), *Spicata* (7)
  Ischnopsyllidae
    Ischnopsyllinae (11): *Hormopsylla* (1), *Myodopsylla* (6), *Nycteridopsylla* (3), *Sternopsylla* (1)
  Leptopsyllidae
    Leptopsyllinae (9): *Leptopsylla* (1), *Peromyscopsylla* (8)
    Amphipsyllinae (9): *Amphipsylla* (3), *Ctenophyllus* (1), *Dolichopsyllus* (1), *Geusibia* (1), *Odontopsyllus* (2), *Ornithophaga* (1)
Superfamily Hystrichopsylloidea
  Ctenophthalmidae
    Anomiopsyllinae (9): *Anomiopsyllus* (9), *Callistopsyllus* (1), *Conorhinopsylla* (2), *Jordanopsylla* (2), *Megarthroglossus* (12), *Stenistomera* (3)
    Ctenophthalminae (3): *Carteretta* (2), *Ctenophthalmus* (1)
    Doratopsyllinae (4): *Corrodopsylla* (3), *Doratopsylla* (1)
    Neopsyllinae (46): *Catallagia* (13), *Delotelis* (2), *Epitedia* (7), *Meringis* (17), *Neopsylla* (1), *Phalacropsylla* (5), *Tamiophila* (1)
    Rhadinopsyllinae (28): *Corypsylla* (3), *Nearctopsylla* (12), *Paratyphloceras* (1), *Rhadinopsylla* (11), *Trichopsylloides* (1)
    Stenoponiinae (2): *Stenoponia* (2)
  Hystrichopsyllidae
    Hystrichopsyllinae (7): *Atyphloceras* (3), *Hystrichopsylla* (4)
Superfamily Malacopsylloidea
  Rhopalopsyllidae
    Rhopalopsyllinae (4): *Polygenis* (3), *Rhopalopsyllus* (1)
Superfamily Pulicoidea
  Pulicidae
    Archaeopsyllinae (2): *Ctenocephalides* (2)
    Hectopsyllinae (2): *Hectopsylla* (2)
    Pulicinae (4): *Echidnophaga* (1), *Pulex* (3)
    Spilopsyllinae (5): *Actenopsylla* (1), *Euhoplopsyllus* (1), *Hoplopsyllus* (1), *Spilopsyllus* (2)
    Tunginae (2): *Tunga* (2)
    Xenopsyllinae (1): *Xenopsylla* (1)
Superfamily Vermipsylloidea
  Vermipsyllidae
    Vermipsyllinae (6): *Chaetopsylla* (6)

Key to Families and Subfamilies of Siphonaptera

1.	Middle coxa without an outer internal ridge (Figures 31–1, 31–7); hind tibia without an apical tooth; sensilium with 8 or 14 pits per side (family Pulicidae)	**15**
1′.	Middle coxa with outer internal ridge (Figures 31–4 – 31–6); hind tibia usually with an apical tooth; sensilium usually with more than 16 pits per side	**2**

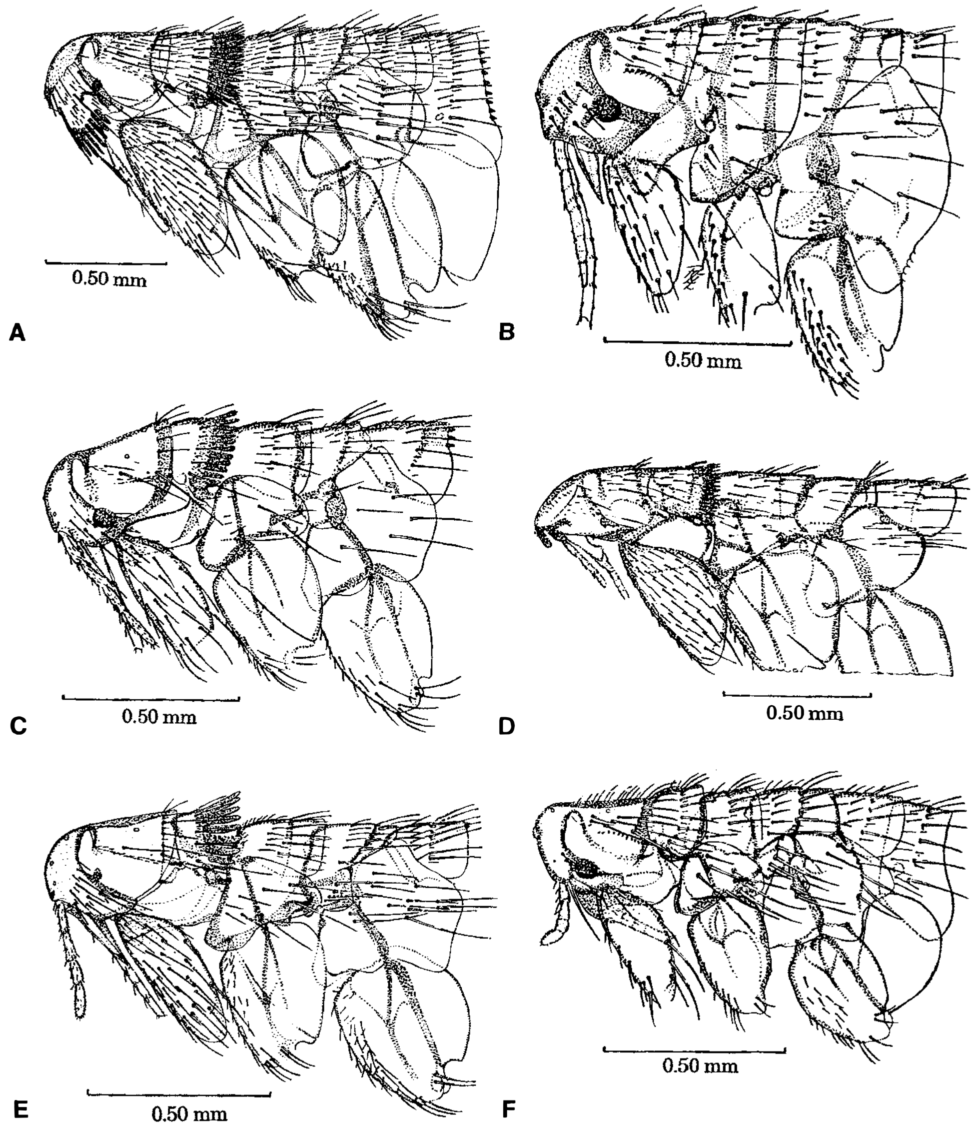


Figure 31–4 Head and thorax of North American representatives of subfamilies of fleas. A, *Hystrichopsylla dippiei* Rothschild (Hystrichopsyllidae); B, *Polygenis gwyni* (C. Fox) (Rhopalopsyllidae); C, *Ceratophyllus gallinae* (Schrank) (Ceratophyllidae, Ceratophyllinae); **D**, *Myodopsylla insignis* (Rothschild) (Ischnopsyllidae); E, *Foxella ignota* (Baker) (Ceratophyllidae, Dactylopsyllinae); F, *Chaetopsylla lotoris* (Stewart) (Vermipsyllidae). (Figure prepared by Robert E. Lewis.)

2(1′). Anterior tentorial arm present in front of eye; genal and pronotal combs absent; mesopleural rod not forked dorsally; ventral margin of pronotum not bilobed; fifth tarsal segment with 4 pairs of plantar bristles; frontal tubercle arising in a groove, its apex directed forward and upward (Figure 31–4B) Rhopalopsyllidae p. 658

2′. Not with the preceding combination of characters 3

3(2′).	Combs, marginal spinelets, antesensilial bristles, spiniform bristles on inner side of hind coxae and anal stylets of female all absent (parasites of carnivores) (Figure 31–4F)	**Vermipsyllidae**	p. 659
3′.	Some or most of the preceding structures present	4	
4(3′).	Mesonotum with marginal spinelets; dorsal surface of sensilium flat; females with 1 spermatheca	5	
4′.	Mesonotum without marginal spinelets; dorsal surface of sensilium more or less convex; females with 1 or 2 spermathecae	7	
5(4).	Interantennal suture well developed; genal comb consisting of 2 broad, blunt spines; eyes absent or vestigial; parasites of bats (Figure 31–4D)	**Ischnopsyllidae**	p. 659
5′.	Interantennal suture usually weak or absent; genal comb never present; no tentorial arch in front of eye; eye present though occasionally reduced, or vestigial (Figure 31–4C,E) (parasites of animals other than bats, mostly of rodents, some birds) (family Ceratophyllidae)	6	
6(5′).	Eye always present, though somewhat reduced in a few cases, circular or ovate, its center sometimes almost transparent (Figure 31–4C) (mainly Holarctic in distribution on rodents and birds)	**Ceratophyllinae**	p. 658
6′.	Eye very much reduced to small, oval and unpigmented (exclusively Nearctic on pocket gophers; Geomyidae) (Figure 31–4E)	**Dactylopsyllinae**	p. 658
7(4′).	Interantennal suture and genal comb present; eye present, often sinuate; pronotal comb always present; occipital tuber absent; marginal or submarginal spinelets present (except in *Ornithophaga*) (Figure 31–5A,B) (family Leptopsyllidae)	8	
7′.	Not with preceding combination of characters	9	
8(7′)	Head always fracticipit; genal comb always present (Figure 31–5A)	**Leptopsyllinae**	p. 658
8′.	Head always integricipit; genal comb always absent (vestigial in *Ornithophaga*) (Figure 31–5B)	**Amphipsyllinae**	p. 658
9(7′)	Club of male antenna extending onto the prosternosome, sensilium strongly convex; females with 2 spermathecae (Figure 31–4A)	**Hystrichopsyllidae**	p. 658
9′.	Club of male antenna not extending onto the prosternosome; sensilium not so strongly convex; females with 1 spermatheca (Figure 31–6) (family Ctenophthalmidae)	10	

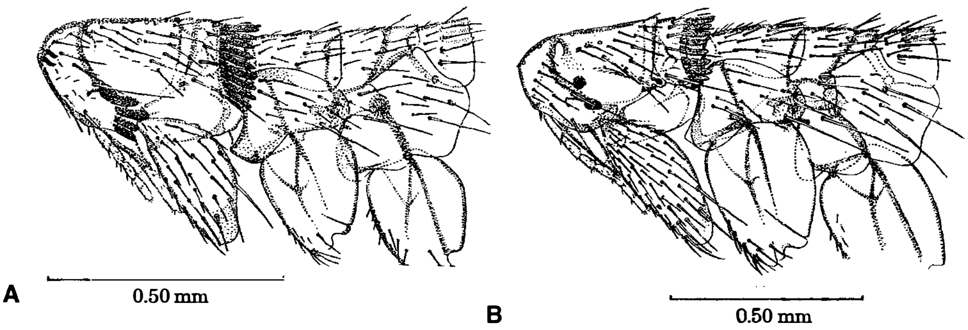


Figure 31–5 Head and thorax of North American representatives of subfamilies of fleas. A, *Leptopsylla segnis* (Schönherr) (Leptopsyllidae, Leptopsyllinae); B, *Amphipsylla sibirica* (Wagner) (Leptopsyllidae, Amphipsyllinae). (Figure prepared by Robert E. Lewis.)

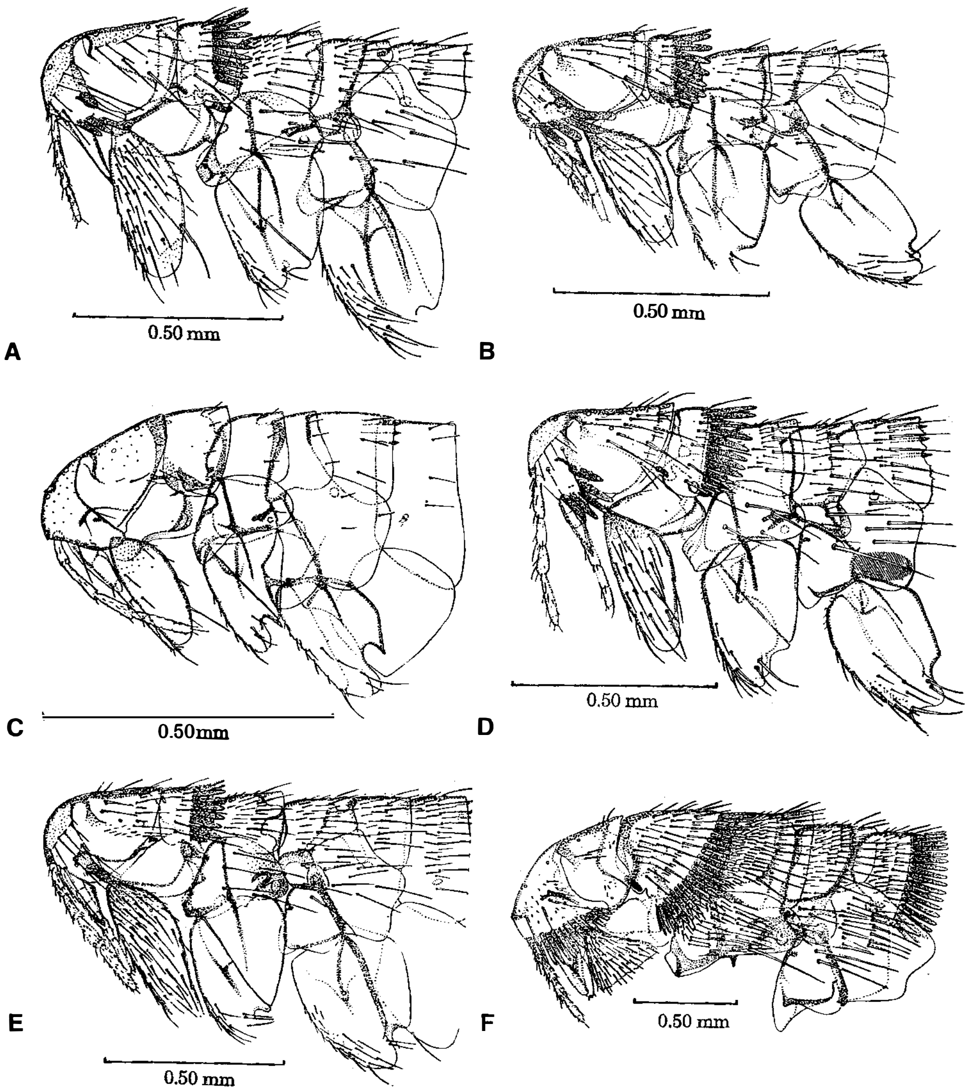


Figure 31–6 Head and thorax of North American representatives of subfamilies of fleas. A, *Ctenophthalmus pseudogyrtes* Baker (Ctenophthalmidae, Ctenophthalminae); B, *Doratopsylla blarinae* C. Fox (Ctenophthalmidae, Doratopsyllinae); C, *Anomiopsyllus montanus* Collins (Ctenophthalmidae, Anomiopsyllinae); D, *Rhadinopsylla fraterna* Baker (Ctenophthalmidae, Rhadinopsyllinae); E, *Neopsylla inopina* Rothschild (Ctenophthalmidae, Neopsyllinae); F, *Stenoponia americana* (Baker) (Ctenophthalmidae, Stenoponiinae). (Figure prepared by Robert E. Lewis.)

10(9′) Labial palpi with at most 2 distinct segments; genal comb well developed, with at least 9 spines, tergite 1 of abdomen with a well-developed comb (Figure 31–6F) (parasites mainly of small rodents) Stenoponiinae p. 658

10′. Labial palpi with at least 4 segments; genal comb sometimes absent, when present rarely with as many as 9 spines; abdomen generally without combs 11

11(10′).	Club of antenna with some segments partially or completely fused so as to appear to consist of only 7 or 8 segments; pleural ridge of metathorax short, more or less broken up or absent; striarium, if present, on metepimeron (Figure 31–6D) (mainly on small mammals, especially rodents)	**Rhadinopsyllinae**	p. 658
11′.	Club of antenna nearly always with 9 distinct segments; pleural ridge of metathorax complete	12	
12(11′).	Genal comb absent; pronotum and tergites 2–7 each with only 1 row of bristles, the anterior row vestigial (Figure 31–6C) (on small rodents)	**Anomiopsyllinae**	p. 658
12′.	Either genal comb well developed or tergites 2–7 each with at least 2 well-developed rows of bristles, or both	13	
13(12′).	Genal comb of 2 overlapping spines or absent; if absent, with striarium on basal abdominal segment (Figure 31–6E) (on small rodents)	**Neopsyllinae**	p. 658
13′.	Genal comb of some other type or absent; if absent, striarium also absent	14	
14(13′).	Genal comb with 4 well-developed and uniformly spaced spines, none arising behind the eye; sensilium with 13 pits per side (Figure 31–6B) (mainly on rodents)	**Doratopsyllinae**	p. 658
14′.	Genal comb not as in preceding entry: reduced to 3 or 5 spines, 1 concealed behind another in lateral view, or with 1 spine arising behind eye; sensilium with more that 13 pits per side (Figure 31–6A) (mainly on small rodents)	Ctenophthalminae	p. 658
15(1).	Inner side of hind coxae without spiniform bristles; sensilium with 8 pits per side; small fleas with heavily barbed mouthparts	16	
15′.	Inner side of hind coxae with spiniform bristles; sensilium with 14 pits per side; larger fleas with mouthparts less barbed	17	
16(15).	Anterior apical angle of hind coxa projecting ventrad as a broad tooth; no tooth at base of hind femur; male genitalia with process of the clasper resembling a pair of opposing claws; spiracles on female abdominal segments 2–4 minute, vestigial, those on 5–8 much enlarged; tropical (Figure 31–7F)	**Tunginae**	p. 659
16′.	Anterior angle of hind coxa without apical tooth; hind femur with large basal tooth; male genitalia with body of clasper short, posteriorly with 3 processes, 1 large and trapeziform, the others forming a pair of pincers; female spiracles on abdominal segments 2–7 of equal size (Figure 31–7E)	Hectopsyllinae	p. 659
17(15′).	Club of antenna asymmetrical, the anterior segments foliaceous and slanting caudad	18	
17′.	Club of antenna symmetrical, elliptical in outline (Figure 31–7C)	Spilopsyllinae	p. 659
18(17).	Pleural rod of mesothorax absent (Figure 31–7A)	**Pulicinae**	p. 659
18′.	Pleural rod of mesothorax present	19	
19(18′).	Falx strongly sclerotized; with both a genal and pronotal comb (Figure 31–7D)	**Archaeopsyllinae**	p. 659
19′.	Falx absent or feebly sclerotized; neither genal nor pronotal comb present (Figure 31–7B)	Xenopsyllinae	p. 659

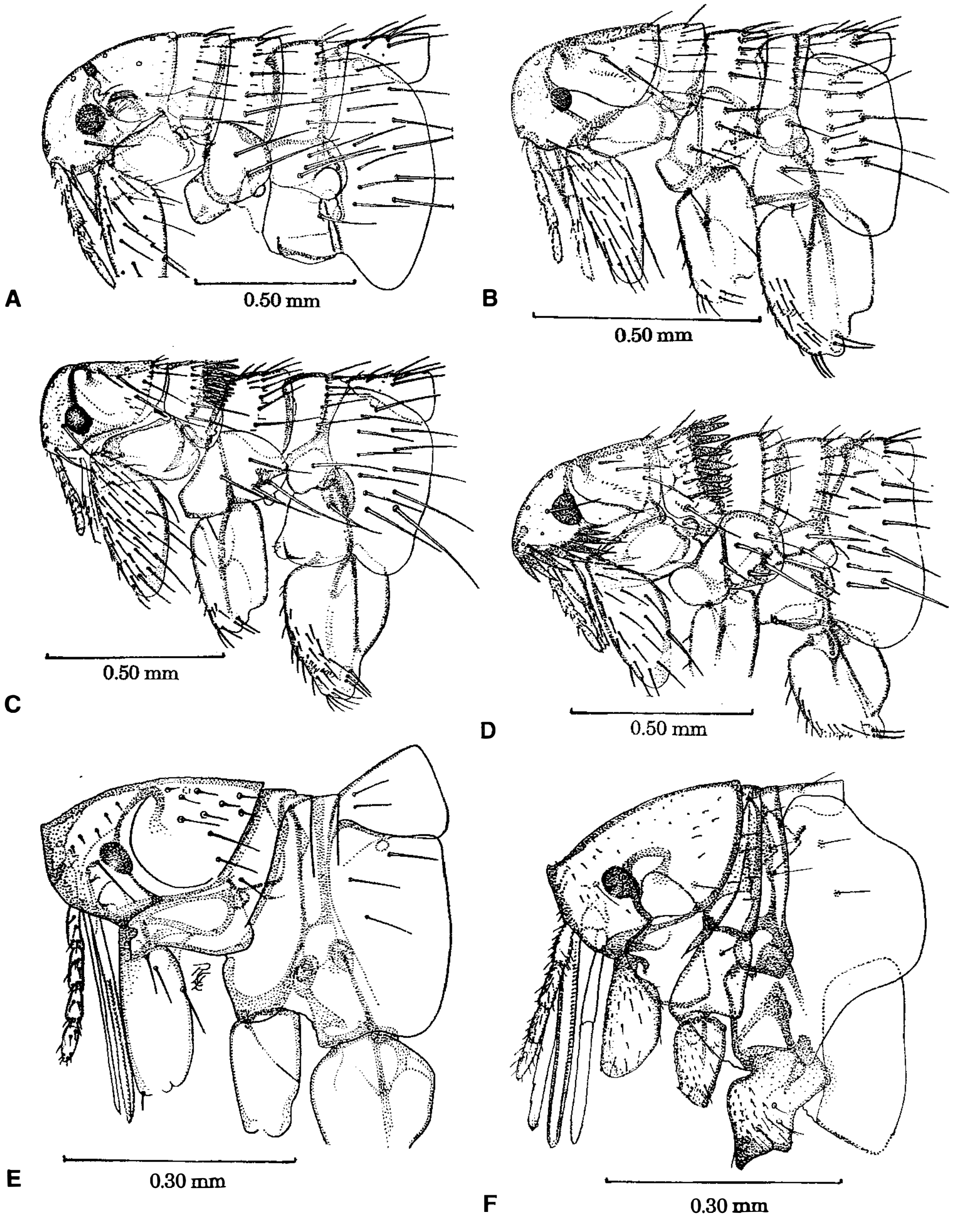


Figure 31–7 Head and thorax of North American representatives of subfamilies of fleas. A, *Pulex irritans* L. (Pulicidae, Pulicinae); B, *Xenopsylla cheopis* (Rothschild) (Pulicidae, Xenopsyllinae); C, *Euholopsyllus glacialis* (Taschenberg) (Pulicidae, Spilopsyllinae); D, *Ctenocephalides felis* (Bouché) (Pulicidae, Archaeopsyllinae); E, *Hectopsylla psittaci* Frauenfeld (Pulicidae, Hectopsyllinae); F, *Tunga penetrans* L. (Pulicidae, Tunginae). (Figure prepared by Robert E. Lewis.)

Family **Ceratophyllidae:** This is the largest family of fleas in North America, with 125 species belonging to 28 genera. Given that only 45 genera are recognized in the world fauna as a whole, this seems to be a relatively young family, geologically, that is rapidly evolving (Traub et al. 1983). Using geological evidence, including zoogeography, these authors posited that ceratophyllids have arisen from leptopsyllid ancestors, that they coevolved on sciurid hosts during the Oligocene, and that this took place in what is now the Nearctic region. The Leptopsyllidae, a more ancient family, are thought to have arisen and evolved in the Palearctic region, perhaps from some hystrichopsylloid ancestor.

Subfamily Ceratophyllinae: The 112 species belonging to this subfamily are distributed in 25 genera. A number are monotypic or with only two or three species. Many show fairly high degrees of host specificity, for example, *Thrassis* species on burrow-dwelling sciurids, *Ceratophyllus* species on various birds, and a number of genera associated with small microtine and cricetid rodents. Most species are distributed in western North America, but a few show a true Holarctic distribution.

Subfamily Dactylopsyllinae: This small subfamily consists of three genera and 15 species, all restricted to the Nearctic Region, and specific parasites of pocket gophers (*Geomys* and *Thomomys* species). One species, *Foxella ignota* (Baker), has the broadest distribution of any in the subfamily. It has been divided into a number of subspecies, most of which are not valid taxa.

Family **Ischnopsyllidae:** This is an unique group of fleas consisting of 11 species in four genera. All are exclusively parasites of bats, mostly vespertilionids, roosting in mines and natural caverns in the rocks. Evidence suggests that the reproductive cycle in this family is mainly influenced by seasonal changes, at least in temperate climates.

Family **Leptopsyllidae:** Of the 240 species in the world fauna assigned to this family, only 18 (7%) are found in North America. Most are in the Palearctic Region, and the North American species are mainly restricted to the western part of the continent. One European species, *Leptopsylla segnis* (Schönherr) is cosmopolitan on *Mus musculus,* the house mouse. *Dolichopsyllus stylosus* is a parasite of the mountain beaver. The majority of other species are associated with small rodents, especially microtines. Evolutionary affinities are discussed briefly under the Ceratophyllidae.

Subfamily Leptopsyllinae: Only nine taxa belong to this subfamily, and one, *Leptopsylla segnis* Schönherr, is not native. The remaining eight species belong to *Peromyscopsylla,* parasites of small rodents.

Subfamily Amphipsyllinae: The six genera and nine species in North America belonging to this subfamily are mostly parasites of small mammals. Most belong to typically Palearctic genera, but the "relict" distribution of *Dolichopsyllus* and *Odontopsyllus* species, if that is what it is, defies logical explanation. *Ornithophaga anomala* Mikulin is a Holarctic parasite of birds, probably woodpeckers.

Family **Ctenophthalmidae:** In North America 112 species are assigned to this taxon, making it the second largest of the Nearctic families. The six subfamilies assigned here are all parasites of small rodents and insectivores.

Subfamily Anomiopsyllinae: One of the 29 North American members of this subfamily is a parasite of flying squirrels (*Glaucomys volans* and *G. sabrinus*) in the East. The remaining species are western, and most are associated with small rodents, especially *Neotoma* (woodrat) species.

Subfamily Ctenophthalminae: Only three species of this large subfamily are found in the Nearctic region. The two species of *Carteretta* parasitize small rodents in the Southwest. *Ctenophthalmus pseudagyrtes* Baker is widespread east of the Rocky Mountains on a broad range of hosts, although it is found primarily on small, microtine rodents.

Subfamily Doratopsyllinae: The four species assigned here are all associated with shrews (*Blarina* and *Sorex* species) as their preferred hosts.

Subfamily Neopsyllinae: This subfamily is well represented in North America, with 46 recognized species. The bulk of these occur in the West, with only 5 or 6 distributed east of the Mississippi River. All are chiefly parasites of small rodents: chipmunks, *Tamias* spp.; ground squirrels, *Spermophilus* spp.; cricetid rodents; woodrats, *Neotoma* spp.; and deer mice, *Peromyscus* spp.

Subfamily Rhadinopsyllinae: Most of the 28 members of this group are distributed in the West, where they are parasites of shrews, moles, and small rodents. Two monotypic genera, *Paratyphloceras oregonensis* Ewing and *Trichopsylloides oregonensis* Ewing, are also specific parasites of the endangered mountain beaver. As a group, the species appear to be nest fleas and winter as adults.

Subfamily Stenoponiinae: The two species assigned here are large fleas found on small rodents, one species in the East, the other in the West.

Family **Hystrichopsyllidae:** As defined here, this family contains seven Nearctic species that are mainly associated with small rodents and insectivores. One species, *Hystrichopsylla schefferi* Chapin, is a parasite of the primitive rodent *Aplodontia rufa,* the mountain beaver, distributed from northern California to southern British Columbia. This species bears the distinction of being the largest flea (8–10 mm long) in the world.

Family **Rhopalopsyllidae:** Only 4 out of the 122 species belonging to the world fauna occur in North

America. They are parasites of armadillos, opossums, and various small rodents.

***Family* Pulicidae:** Diverse though this assemblage is, historically the separate elements—whether assigned to the level of family, subfamily, or tribe—have been acknowledged to be phylogenetically closer to each other than to other taxa in the order. Currently this family in the world fauna has 181 species in 27 genera. Of these, 16 are known from North America. They are assigned to the following subfamilies.

Subfamily Archaeopsyllinae: The only two North American taxa, *Ctenocephalides felis* (Bouché) and *C. canis* (Curtis), are not native to North America. The former is a pest of domestic pets and livestock, and frequently becomes a household pest. In the past decade, researchers have made major developments in flea control using juvenile growth hormones, and this has been the experimental species. The latter taxon is much less common. Both are known as intermediate hosts of the dog tapeworm, *Dipylidium caninum*.

Subfamily Hectopsyllinae: This tropical group is usually associated with rodents and other small mammals. The North American species *Hectopsylla psittacei* Frauenfeld is a parasite of cliff swallows (*Petrochelidon pyrrhonota*) in California.

Subfamily Pulicinae: Only four species belonging to two genera in this family occur in North America. The sticktight flea, *Echidnophaga gallinacea* (Westwood), can be a pest of domestic poultry, but also infests medium-sized mammals and wild birds. Adults tend to congregate in areas on the host that are difficult to groom and may remain attached for extended periods. *Pulex porcinus* Jordan and Rothschild is a common parasite of peccaries, *Pecari tajacu*. The other two species of *Pulex*, *P. irritans* Linnaeus and *P. simulans* Baker, infest a broad range of hosts from small to medium-sized mammals, and the former is sometimes associated with human habitations.

Subfamily Spilopsyllinae: The five species in this subfamily belong to four genera. One species is a parasite of hole-nesting birds on both coasts of North America. The other four are found on rabbits and hares. Evidence suggests that at least *Spilopsyllus simplex* (Baker) and *S. inaequalis* (Baker) have developed an elaborate physiological mechanism whereby the reproductive cycle of the flea depends on the reproductive cycle of the host. The process is described in detail by Marshall (1981) based on the studies of Rothschild and her associates with the European rabbit flea, *S. cuniculi* (Dale).

Subfamily Tunginae: Females in this subfamily become permanent parasites during the adult stage. Whereas adult males are small, short-lived, and evidently do not feed, on attachment females become encapsulated by the host's tissues and remain in situ for the rest of their lives. Of the two species included here, *Tunga penetrans* (L.) and *T. monositus* Barnes and Radovsky, only the latter has been established with certainty in North America (Hastriter 1997). In both cases, the attachment of the female triggers a response in the host's tissues, ultimately causing complete encapsulation of the flea except for the terminal abdominal segments, which remain open to the exterior via a small pore in the capsule. Nourished by tissue fluids secreted by the host, the abdomen of the female flea enlarges by as much as 1,000× (about the size of a garden pea), accompanied by the production of large quantities of eggs, which are discharged through the pore in the capsule, where they fall to the ground and begin their development. After a full complement of approximately 100 eggs has been produced, the dead body of the female is usually discharged from the host by pressure from the surrounding tissues. Females of *T. penetrans* usually attach between the toes and under the toenails in human hosts. The sites, if untreated, may become septic or cause other medical problems.

Subfamily Xenopsyllinae: Most members of this subfamily are native to Africa, Asia, or Australia. However, *Xenopsylla cheopis* (Rothschild), the Oriental rat flea, is cosmopolitan, having been transported (by human agency) on black and Norway rats (*Rattus rattus* and *R. norvegicus*). This flea is generally credited historically with being the major vector of bubonic plague during the early pandemics in Asia and Europe. Today it does not figure prominently in maintaining sylvatic plague in nature. However, it is an intermediate host to the tapeworm *Hymenolepis diminuta*.

***Family* Vermipsyllidae:** This family contains only three genera in the world fauna, including 6 species of the genus *Chaetopsylla* in North America. All are associated with various carnivores (for example, raccoons, foxes, wolves, and bears) and all tend to be distributed in the colder parts of the Nearctic and Palearctic regions.

Collecting and Preserving Siphonaptera

Fleas can be collected from host animals or from their nests or lair. The methods suggested for collecting Phthiraptera also apply to the Siphonaptera.

Fleas should be preserved in 75% ethyl alcohol, although a good alternative is to store them dry in small vials, held in place by nonabsorbent cotton. Never preserve adults in a formaldehyde-based preservative, because these tend to fix the tissues in a way that makes it impossible to properly clear the fleas for study on microscope slides.

Mammal nests are usually difficult to find, but once located they may continue to yield adults for extended periods if not permitted to dry out. Bird nests are usually more easily located, but most nests in open areas do not contain fleas. The most productive nests are those in burrows or natural cavities in the ground, in holes in trees, or mud nests on buildings or cliff faces. Examine nest material by placing it on a white background and thoroughly picking it apart. Live fleas and other nidicolous invertebrates can be picked up with an aspirator or with a camel's-hair brush wetted with alcohol. Keep nesting material for a few weeks, preferably in a paper bag or other reasonably porous container, at room temperature, moisten it periodically and examine it every few days for newly emerged adults.

In areas where adults are particularly abundant, such as yards and outbuildings, adults can be collected with a white cloth, or you can simply walk about the area collecting adults as they jump on your clothing. In the latter case, fleas are most visible on light-colored clothing.

References

Adams, N. E., and R. E. Lewis. 1995. An annotated catalogue of primary types of Siphonaptera in the National Museum of Natural History, Smithsonian Institution. Smithson. Contrib. Zool. 560:1–86.

Cheetham, T. B. 1988. Male genitalia and the phylogeny of the Pulicoidea (Siphonaptera). Theses Zool. 8:1–221.

Elbel, R. E. 1991. Order Siphonaptera. In F Stehr (Ed.), Immature Insects, vol. 2, pp. 674–689. Dubuque, IA: Kendall/Hunt.

Ewing, H. E., and I. Fox. 1943. The fleas of North America. Classification, identification, and geographic distribution of these injurious and disease-spreading insects. U.S. Dept. Agric. Misc. Publ. 500:1–143.

Fox, I. 1940. Fleas of Eastern United States. Ames: Iowa State College Press. 191 pp.

Hastriter, M. W. 1997. Establishment of the tungid flea, *Tunga monositus* (Siphonaptera: Pulicidae) in the United States. Great Basin Nat. 53:281–283.

Holland, G. P. 1985. The fleas of Canada, Alaska and Greenland. Mem. Entomol. Soc. Can. 130:1–631.

Hopkins, G. H. E., and M. Rothschild. 1953–1971. An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History). Vol. 1 (1953): Tungidae and Pulicidae. Vol 2 (1956): Coptopsyllidae, Vermipsyllidae, Stephanocircidae, Ischnopsyllidae, Hypsophthalmidae and Xipiopsyllidae [and Macropsyllidae]. Vol. 3 (1962): Hystrichopsyllidae (Acedestinae, . . .). Vol. 4 (1966): Hystrichopsyllidae (Ctentophthalminae, . . .). Vol. 5 (1971): (Leptopsyllidae and Ancistropsyllidae). London: British Museum (Natural History).

Hubbard, C. A. 1947. Fleas of Western North America. Ames: Iowa State College Press, 533 pp.

Lewis, R. E. 1972–1974. Notes on the geographical distribution and host preferences in the order Siphonaptera. 1972. Part 1: Pulicidae. 1973. J. Med. Entomol. 9:511–520. Part 2: Rhopalopsyllidae, Malacopsyllidae and Vermipsyllidae. 1974. J. Med. Entomol. 10:255–260. Part 3: Hystrichopsyllidae. J. Med. Entomol. 11:147–167. Part 4: Coptopsyllidae, Pygiopsyllidae, Stephanocircidae and Xiphiopsyllidae. J. Med. Entomol. 11:403–413. Part 5: Ancistropsyllidae, Chimaeropsyllidae, Ischnopsyllidae, Leptopsyllidae and Macropsyllidae. J. Med. Entomol. 11:525–540. Part 6: Ceratophyllidae. J. Med. Entomol. J. Med. Entomol. 11:658–676.

Lewis, R. E. 1990. The Ceratophyllidae: Currently accepted valid taxa (Insecta: Siphonaptera). Theses Zool. 13:1–267.

Lewis, R. E. 1993. Fleas (Siphonaptera). In R. P. Lane and R. W. Crosskey (Eds.), Medical Insects and Arachnids, pp. 529–575. London: Chapman & Hall.

Lewis, R. E. 1998. Résumé of the Siphonaptera (Insecta) of the world. J. Med. Entomol. 35:377–389.

Lewis, R. E., and T. D. Galloway. 2002. A taxonomic review of the *Ceratophyllus* Curtis, 1832 of North America (Siphonaptera: Ceratophyllidae: Ceratophyllinae). J. Vector Ecol. 26:119–161.

Lewis, R. E., and D. Grimaldi. 1997. A pulicid flea in Miocene amber from the Dominican Republic (Insecta: Siphonaptera: Pulicidae). Am. Mus. Novit. 3205:1–9.

Lewis, R. E., and J. H. Lewis. 1985. Notes on the geographical distribution and host preferences in the order Siphonaptera. Part 7: New taxa described between 1972 and 1983, with a superspecific classification of the order. J. Med. Entomol. 22:134–152.

Lewis, R. E., and J. H. Lewis. 1989. Catalogue of invalid genus-group and species-group names in Siphonaptera (Insecta). Theses Zool. 11:1–263.

Lewis, R. E., and J. H. Lewis. 1985. Notes on the geographical distribution and host preferences in the order Siphonaptera. Part 8: New taxa described between 1984 and 1990, with a current classification of the order. J. Med. Entomol. 30:239–256.

Lewis, R. E., and J. H. Lewis. 1994a. Siphonaptera of North America north of Mexico: Vermipsyllidae and Rhopalopsyllidae. J. Med. Entomol. 31:82–98.

Lewis, R. E., and J. H. Lewis. 1994b. Siphonaptera of North America north of Mexico: Ischnopsyllidae. J. Med. Entomol. 31:348–368.

Lewis, R. E., and J. H. Lewis. 1994c. Siphonaptera of North America north of Mexico: Hystrichopsyllidae *s. str.* J. Med. Entomol. 31:795–812.

Lewis, R. E., J. H. Lewis, and C. Maser. 1988. The Fleas of the Pacific Northwest. Corvallis: Oregon State University Press, 296 pp.

Marshall, A. G. 1981. The Ecology of Ectoparasitic Insects. London: Academic Press, 459 pp.

Peus, F. 1956. Siphonaptera. In S. L. Tuxen (Ed.), Taxonomist's Glossary of Genitalia in Insects, pp. 122–131. Copenhagen: Munksgaard.

Pilgrim, R. L. C. 1991. External morphology of flea larvae (Siphonaptera) and its significance in taxonomy. Fla. Entomol. 74:386–395.

Rothschild, M. 1975. Recent advances in our knowledge of the order Siphonaptera. Ann. Rev. Entomol. 20:241–259.

Smit, F. G. A. M. 1970. Siphonaptera. In S. L. Tuxen (Ed.), Taxonomist's Glossary of Genitalia in Insects, 2nd ed., pp. 141–156.. Copenhagen: Munksgaard.

Smit, F. G. A. M. 1982. Siphonaptera. In S. P. Parker (Ed.), Synopsis and Classification of Living Organisms, vol. 2, pp. 557–563. New York: McGraw-Hill.

Smit, F. G. A. M. 1983. Key to the genera and subgenera of Ceratophyllidae. In R. Traub, M. Rothschild, and J. F. Haddow (Eds.), The Rothschild Collection of Fleas. The family Ceratophyllidae: Key to the genera and host relationships, with notes on their evolution, zoogeography and medical importance, pp. 1–41. Cambridge, UK: Cambridge University Press.

Smit, F. G. A. M. 1987. An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History). Vol. 7: Malacopsylloidea (Malacopsyllidae and Rhopalopsyllidae). Oxford, UK: Oxford University Press,

Smit, F. G. A. M., and A. M. Wright. 1978. A catalogue of primary type-specimens of Siphonaptera in the British Museum (Natural History). London: British Museum (Natural History), 71 pp. (Mimeographed).

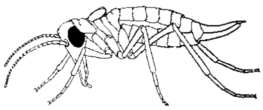
Snodgrass, R. E. 1946. The skeletal anatomy of fleas (Siphonaptera). Smithson. Misc. Coll. 104:1–89.

Traub, R. 1950. Siphonaptera from Central America and Mexico. A morphological study of the aedeagus with descriptions of new genera and species. Fieldiana Zool. Mem. 1:1–127.

Traub, R., M. Rothschild, and J. F. Haddow. 1983. The Rothschild Collection of Fleas. The family Ceratophyllidae: Key to the genera and host relationships, with notes on their evolution, zoogeography and medical importance. Cambridge, UK: Cambridge University Press. (distributed by Academic Press, London), 288 pp.

32

Order Mecoptera[1,2]
Scorpionflies and Hangingflies



Scorpionflies and hangingflies are medium-sized (about 9–25 mm long), slender-bodied insects with the head prolonged below the eyes as a beak, or rostrum (Figure 32–1A, 32–2). The rostrum is formed primarily by elongation of the clypeus. Its posterior surface consists partly of the lengthened maxillae and labium, but the mandibles are not unusually elongate and are at the lower end of the rostrum. In the relatively uncommon Panorpodidae, the rostrum is short (Figure 32–5A). Most Mecoptera have four long, narrow, membranous wings. The front and hind wings are similar in size and shape and have similar venation.

The wing venation of Mecoptera is very near the generalized pattern hypothesized by Comstock (1940) (see Figure 2–10), with most of the longitudinal veins and their branches present and with numerous crossveins. A distinctive venational feature of this order is the fusion in the hind wing of Cu_1 with M for a short distance near the wing base, and a similar fusion of Cu_2 with 1A (Figures 32–3, 32–5B). In the front wing of the Bittacidae, likewise, Cu_1 fuses with M for a short distance.

The common name *scorpionflies* is derived from the genital segment of males of the family Panorpidae, which is bulbous and often curved forward above the back, like a scorpion's sting. These insects cannot sting, however, and are quite harmless.

Scorpionflies undergo complete metamorphosis, with fairly rapid development of the larva followed by a prolonged prepupal stage. Pupation occurs in an oblong cell excavated by the larva in the soil. Larvae of Panorpidae and Bittacidae are eruciform, with short, pointed prolegs on abdominal segments 1–8 (Figure 32–1B). Those of Panorpodidae and Boreidae are somewhat scarabaeiform, without prolegs, but they lack tarsal claws and their middle and hind legs project laterally more than do the front legs. Larval Panorpidae are unusual among holometabolous larvae in having compound eyes of approximately 30 ommatidia each. Eyes of bittacid larvae have only 7 ommatidia in a circular cluster, boreids have only 3, and panorpodids are eyeless. The larvae of Meropeidae are unknown.

Mecoptera are judged to be one of the more generalized orders of Holometabola. Fossil Mecoptera appear first in strata of lower Permian age, and at that time Mecoptera were apparently one of the major orders. Many more families and genera are known as fossils than are extant today.

Classification of the Mecoptera

Five families of Mecoptera are represented in North America, and there are four other families, restricted to southern South America and the Australian region. The majority of specimens encountered by general collectors belong to just two families, the Panorpidae and the Bittacidae. Families of Mecoptera are defined largely on the basis of wing venation and tarsal structure, but the classification is supported by details of adult and larval morphology, feeding habits, and other aspects of the biology of the insects.

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[1] Mecoptera: *meco*, long; *ptera*, wings.

[2] This chapter was written by George W. Byers.

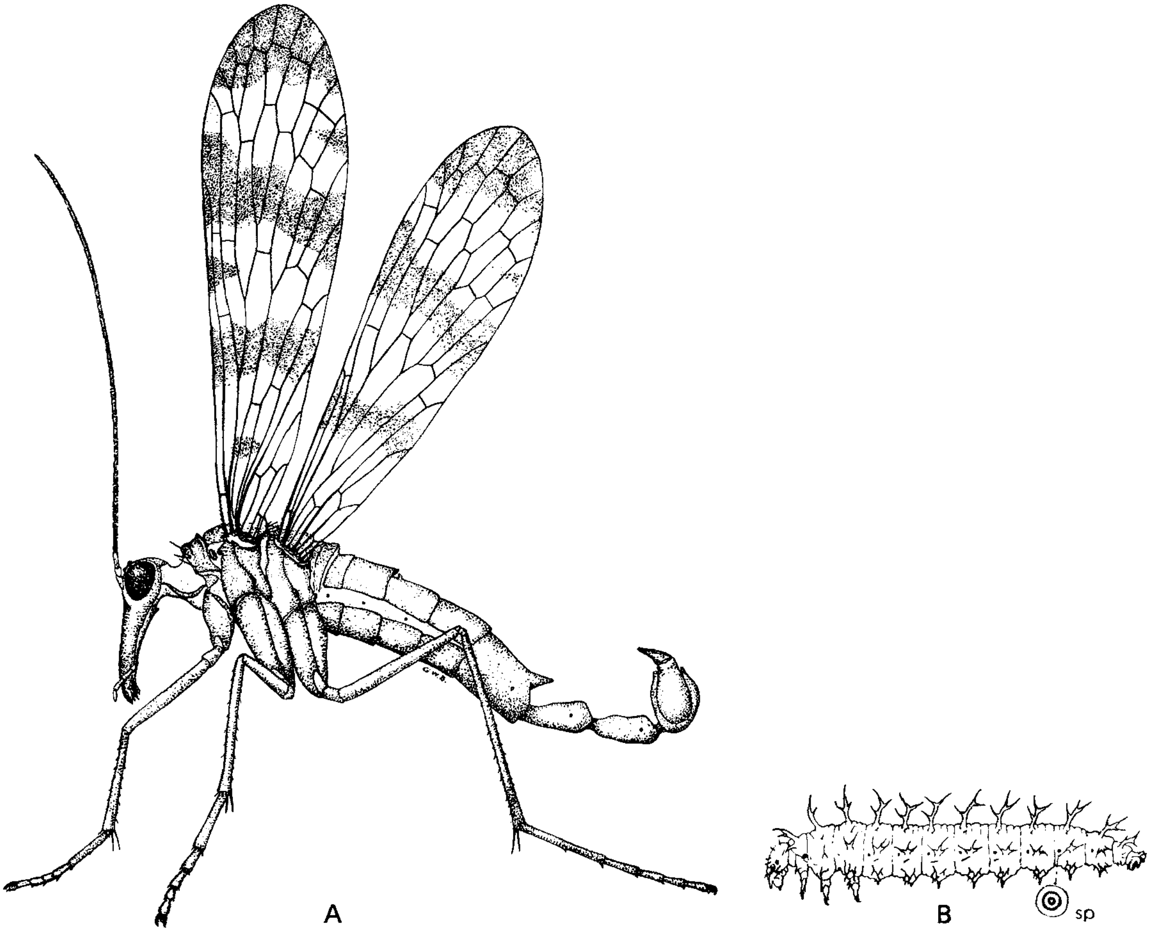


Figure 32–1 A, a male scorpionfly, *Panorpa helena* Byers; B, larva of a hangingfly (*Bittacus*); *sp*, spiracle. (B, courtesy of Peterson, A. 1951. Larvae of Insects. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Ann Arbor, MI: Edwards Bros., 416 pp., reprinted by permission.)

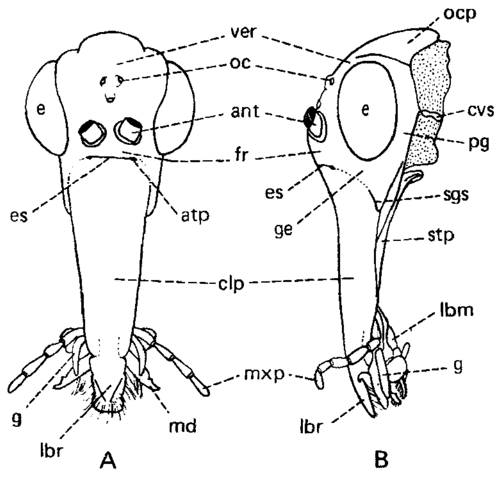


Figure 32–2 Head of *Panorpa*. A, anterior view; B, lateral view. *ant*, antenna; *atp*, anterior tentorial pit; *clp*, clypeus; *cvs*, cervical sclerite; *e*, compound eye; *es*, epistomal sulcus; *fr*, frons; *g*, galea; *ge*, gena; *lbm*, labium; *lbr*, labrum; *md*, mandible; *mxp*, maxillary palp; *oc*, ocelli; *ocp*, occiput; *pg*, postgena; *sgs*, subgenal sulcus; *stp*, stipes; *ver*, vertex. (Redrawn from Ferris, G. F., and B. E. Rees. 1939. The morphology of *Panorpa nuptialis* Gerstaecker (Mecoptera: Panorpidae). Microentomology 4:79–108.)

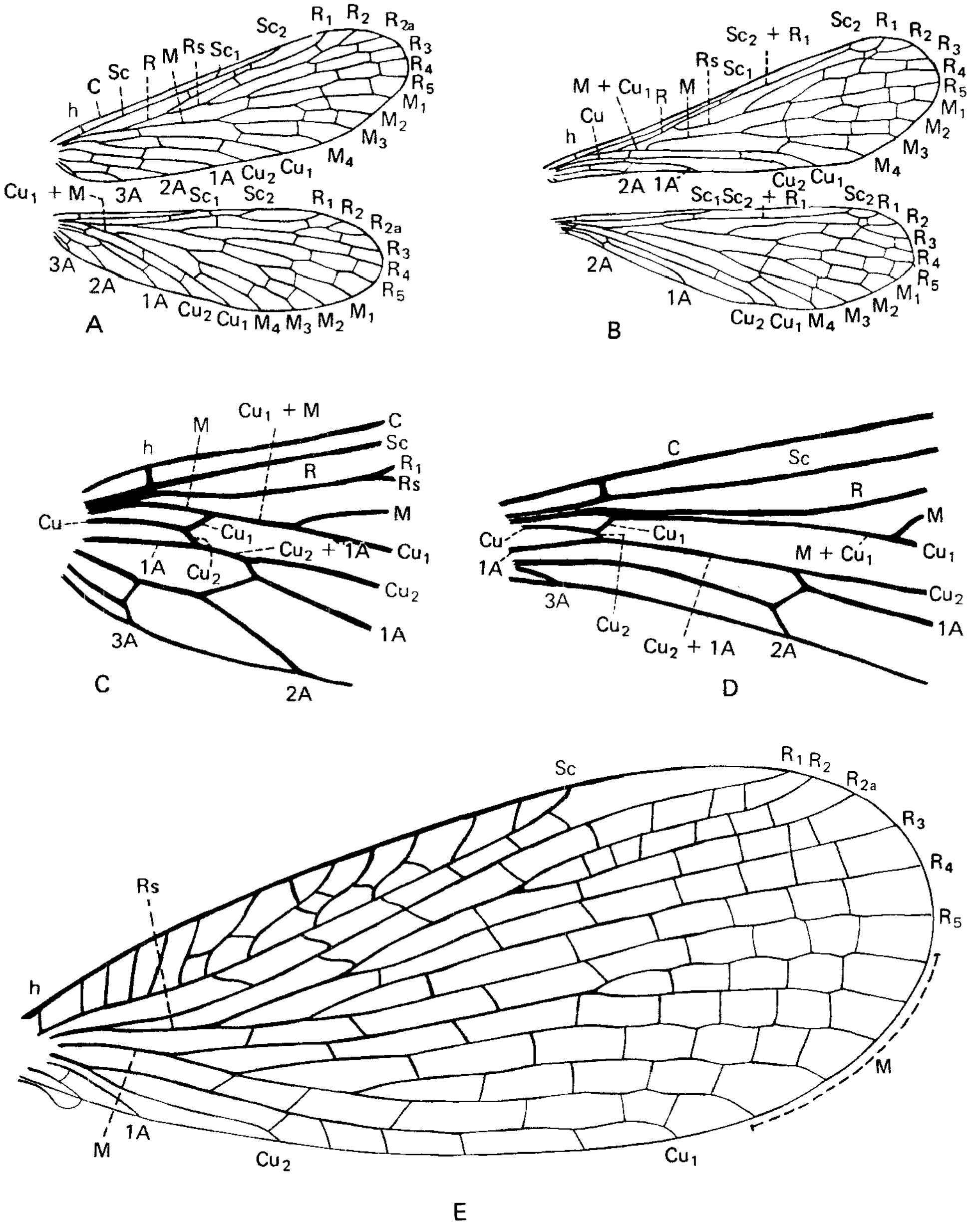


Figure 32–3 Wings of Mecoptera. A, *Panorpa* (Panorpidae); B, *Bittacus* (Bittacidae); C, base of hind wing of *Panorpa*; D, base of hind wing of *Bittacus*; E, front wing of *Merope* (Meropeidae).

Key to the Families of Mecoptera

1.	Tarsi each with one large claw (Figure 32–4B); tarsi raptorial, fifth tarsal segment folding back against fourth	Bittacidae	p. 666
1′.	Tarsi each with 2 small claws (Figure 32–4A); fifth tarsal segment not folding back against fourth	2	

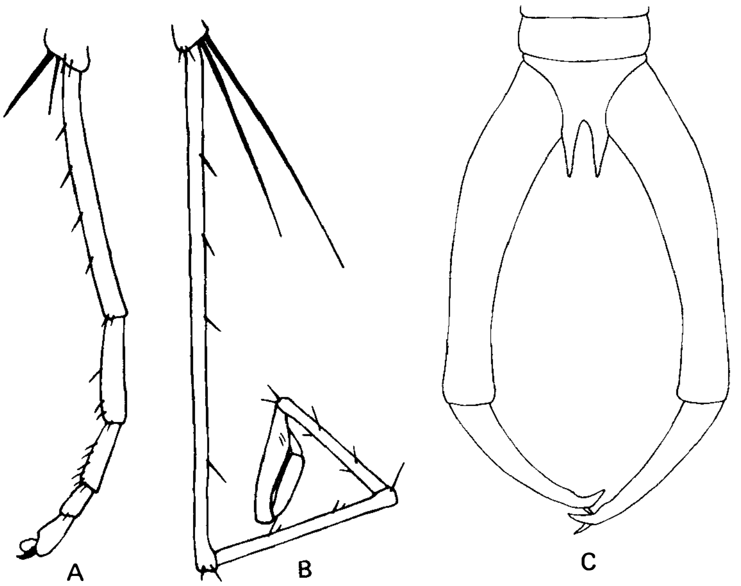


Figure 32–4 A, tarsus of *Panorpa* (Panorpidae); B, tarsus of *Bittacus* (Bittacidae); C, anal appendages of a male *Merope* (Meropeidae).

2(1′).	Wings reduced to hardened, slender hooks in male and to short, roughly oval, sclerotized pads in female (Figure 32–6); small (2–7.4 mm), dark brown to black insects	Boreidae	p. 667
2′.	Wings nearly always well developed and membranous, never sclerotized; body yellowish brown to brown, rarely blackish, 9–25 mm long	3	
3(2′).	Wings narrow, 3.5 or more times as long as their greatest width (if wings reduced, rostrum very short); costal cell without crossveins beyond h (rarely, 1); M with 4 branches (Figures 32–1A, 32–3A, 32–5B); genital claspers of male with bulbous basal segment, cheliform apical segment; ocelli conspicuous, on raised tubercle	4	

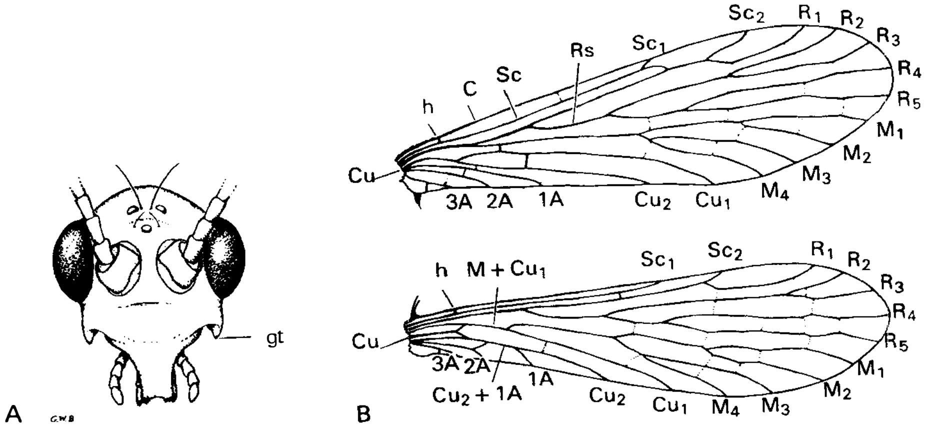


Figure 32–5 Characters of *Brachypanorpa oregonensis* McLachlan (Panorpodidae). A, face of male, anterior view; B, wings of male. *gt*, genal tooth.

3′.	Wings broad, about 2.4 times as long as their greatest width; costal cell with 10 or more crossveins beyond h; M with 5 or more branches, venation reticulate (Figure 32–3E); genital claspers of male with long, slender basal and apical segments (Figure 32–4C); ocelli absent	Meropeidae	p. 666
4(3).	Rostrum elongate, more than twice as long as width at base (Figure 32–2); wings well developed in both sexes, usually patterned with transverse bands or spots; R_2 branched	Panorpidae	p. 666
4′.	Rostrum short, only slightly longer than width at base (Figure 32–5A); wings well developed in males, slightly to greatly reduced in females, uniformly yellowish brown or paler along crossveins; R_2 not branched	Panorpodidae	p. 666

Family **Panorpidae—Common Scorpionflies:** In this family the genital appendages of males are enlarged, forming a bulblike structure that is carried above the back, resembling the sting of a scorpion (Figure 32–1A). The abdomen of the female tapers posteriorly and bears two short, fingerlike, apical cerci. Most of these scorpionflies are dirty yellowish brown, but some are darker brown to nearly black. Their wings are usually transversely banded with interspersed spots, or they may be only spotted. One southeastern species, *Panorpa lugubris* Swederus, is dark reddish brown with almost totally black wings. Although most scorpionflies are 10 to 15 mm long, males of *Panorpa nuptialis* Gerstaecker, of the south-central United States, may attain a length of 25 mm. Scorpionflies are most commonly found on low broad-leaf plants at edges of woods or in open shade beneath deciduous trees. Both adults and larvae feed primarily on dead insects, less often on other dead animal matter. Adults occasionally feed on insects trapped in spiders' webs. Pupation occurs in an oblong cell prepared by the fourth-instar larva just beneath the soil surface. There are 54 species known from eastern North America (southeastern Canada to northern Florida and westward to southern Manitoba and eastern Texas), all in the Holarctic genus *Panorpa*. Several species are widespread, such as *P. helena* Byers (Figure 32–1A), but most have ecologically and geographically restricted ranges.

Family **Bittacidae—Hangingflies:** Bittacids are slender-bodied, about 12–22 mm long, light yellowish brown to reddish brown, with long, slender legs and narrow wings. They resemble large crane flies, particularly in flight. Their wings are narrower near the base than are those of Panorpidae (Figure 32–3A,B). One species in central California, *Apterobittacus apterus* (MacLachlan), is wingless. Unable to stand on surfaces, adult bittacids spend most of their time hanging by their front legs or front and middle legs from stems or edges of leaves. They are predaceous, capturing their prey by means of their raptorial hind tarsi, either while hanging or by flying up plant stems while making sweeping movements of the hind legs. Prey, grasped by the hind tarsi, is then held up to the mouthparts, pierced, and the hemolymph and soft parts sucked out. Their prey includes small, soft-bodied insects such as flies, moths, caterpillars, and aphids, and occasionally spiders. Male hangingflies lure females for mating by emitting a sex-attractant pheromone from everted vesicles on the dorsum of the abdomen and subsequently offering the female a captured prey insect as a nuptial meal (Thornhill 1978).

Seven species of *Bittacus* occur in eastern North America and California. A single species of *Orobittacus*, *O. obscurus* Villagus & Byers, is known from central California. All these bittacids hold the wings alongside the abdomen when suspended. *Hylobittacus apicalis* (Hagen) of the eastern United States hangs with its wings outspread and, unlike the other species, has conspicuously darkened wing tips.

Family **Panorpodidae—Short-Faced Scorpionflies:** Three species of *Brachypanorpa* occur in the southern Appalachian Mountains and two in montane regions of the northwestern United States. These dull yellowish to yellowish brown scorpionflies have a short rostrum (Figure 32–5A). The genital appendages of males are enlarged, as in Panorpidae, but are not carried forward above the back. In one eastern species and two western species, females have rudimentary wings extending only to the base of the abdomen, whereas in the other species in each region the females have wings reaching the base of the abdomen or slightly beyond. The eyeless, somewhat scarabaeiform larvae have been found in soil beneath grassy areas in woods and are presumed to feed on plant matter. Adults scrape surfaces of herbaceous vegetation for nourishment.

Family **Meropeidae—Earwigflies:** A single species, *Merope tuber* Newman, occurs in the eastern United

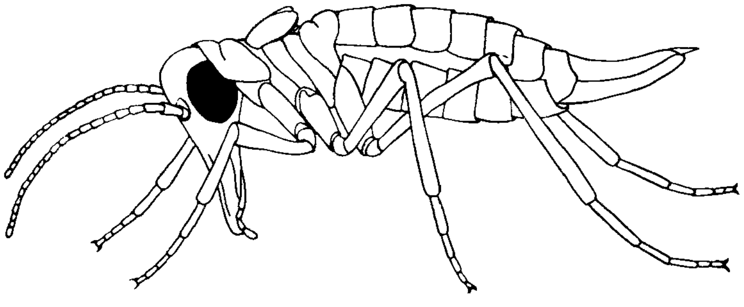


Figure 32–6 A snow scorpionfly, *Boreus brumalis* (Fitch), female.

States and adjacent Canada. It is a dull brownish insect, 10–12 mm long, somewhat flattened, with relatively broad wings having numerous crossveins (Figure 32–3E). The male has greatly elongated, forcepslike claspers at the apex of the abdomen (Figure 32–4C). This species ranges from southeastern Ontario to Georgia and westward to Minnesota and Kansas. It is secretive in habits and is sometimes found beneath logs and rocks. Once regarded as rare, it is fairly frequently taken in Malaise traps. Its only known living relative is a species in southwestern Australia.

***Family* Boreidae—Snow Scorpionflies:** These small insects (2 to 7.4 mm long) reach adult form in winter. They are most often seen on the surface of snow because of their movement and dark, contrasting color. However, they may also be found in mosses on which their larvae feed. The slender, hardened, hooklike wings of the male are used to grasp the female, which is carried on his back, in mating. The family is represented in eastern North America by two species, *Boreus brumalis* Fitch (Figure 32–6), a shiny black species, and *B. nivoriundus* Fitch, which is brown. In the West, there are eight additional species of *Boreus*, the most widespread and common being *B. californicus* Packard; two species of *Hesperoboreus*; and one of the aberrant *Caurinus*.

Collecting and Preserving Mecoptera

Panorpidae and Bittacidae can be readily collected individually with a net. They are rather weak fliers and when alarmed ordinarily fly only a few meters. Sweeping may be effective when the vegetation is not dense, and is almost necessary to obtain the flightless females of *Brachypanorpa*. Boreids may be handpicked from snow surface or extracted from mosses. Malaise traps and chemical traps have proved most useful for catching *Merope*, and may also trap *Panorpa*. Bittacidae often are attracted to lights. Panorpids are usually pinned. Drying bittacids in paper envelopes or folded paper triangles, then gluing them on points, avoids much breakage of legs and wings. Preserve boreids in 75% ethanol or glued onto points.

References

Byers, G. W. 1954. Notes on North American Mecoptera. Ann. Entomol. Soc. Amer. 47:484–510.

Byers, G. W. 1963. The life history of *Panorpa nuptialis* (Mecoptera: Panorpidae). Ann. Entomol. Soc. Amer. 56:142–149.

Byers, G. W. 1965. Families and genera of Mecoptera. Proc. 12th Int. Congr. Entomol. London (1964), p. 123.

Byers, G. W. 1973. Zoogeography of the Meropeidae (Mecoptera). J. Kan. Entomol. Soc. 46:511–516.

Byers, G. W. 1987. Order Mecoptera. In F. W. Stehr (Ed.), Immature Insects, pp. 246–252. Dubuque, IA: Kendall/Hunt, 754 pp.

Byers, G. W., and R. Thornhill. 1983. Biology of the Mecoptera. Annu. Rev. Entomol. 28:203–228.

Carpenter, F. M. 1931. Revision of Nearctic Mecoptera. Bull. Mus. Comp. Zool. Harvard 72:205–277.

Carpenter, F. M. 1931. The biology of the Mecoptera. Psyche 38:41–55.

Cooper, K. W. 1972. A southern California *Boreus*, *B. notoperates*, n. sp. I: Comparative morphology and systematics (Mecoptera: Boreidae). Psyche 79:269–283.

Cooper, K. W. 1974. Sexual biology, chromosomes, development, life histories and parasites of *Boreus*, especially of *B. notoperates*, a southern California *Boreus* (Mecoptera: Boreidae), II. Psyche 81:84–120.

Ferris, G. F., and B. E. Rees. 1939. The morphology of *Panorpa nuptialis* Gerstaecker (Mecoptera: Panorpidae). Microentomology 4:79–108.

Hinton, H. E. 1958. The phylogeny of the panorpoid orders. Annu. Rev. Entomol. 3:181–206.

Kaltenbach, A. 1978. Mecoptera (Schnabelhafte, Schnabelfliegen). Handbuch der Zoologie 4(2) 2/28:1–111. Berlin: de Gruyter.

Penny, N. D. 1977. A systematic study of the family Boreidae (Mecoptera). Univ. Kan. Sci. Bull. 51:141–217.

Peterson, A. 1951. Larvae of Insects. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Ann Arbor, MI: Edwards Bros., 416 pp.

Setty, L. R. 1940. Biology and morphology of some North American Bittacidae. Amer. Midl. Nat. 23(2):257–353.

Thornhill, R. 1978. Sexually selected predatory and mating behavior of the hangingfly *Bittacus stigmaterus* (Mecoptera: Bittacidae). Ann. Entomol. Soc. Amer. 71:597–601. **[cited]**

Tillyard, R. J. 1935. The evolution of the scorpion-flies and their derivatives (Order Mecoptera). Ann. Entomol. Soc. Amer. 28:1–45.

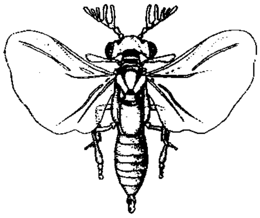
Webb, D. W., N. D. Penny, and J. C. Martin. 1975. The Mecoptera, or scorpionflies, of Illinois. Ill. Nat. Hist. Surv. Bull. 31(7):250–316.

Willmann, R. 1987. The phylogenetic system of the Mecoptera. Syst. Entomol. 12:519–524.

33

Order Strepsiptera[1]

Twisted-Wing Parasites



The Strepsiptera are minute insects, all of which are parasitic on other insects. The two sexes are quite different; the males are free-living and winged, whereas the females are wingless and often legless, and in most species do not leave the host.

Male Strepsiptera (Figure 33–1A–D) are somewhat beetlelike in appearance, with protruding, raspberry-like eyes, and the antennae often have elongate processes on some segments. The front wings are reduced to clublike structures that resemble the halteres of the Diptera. The hind wings are large and membranous, fanlike, and have a reduced venation (only longitudinal veins). The adult females of the Old World family Mengenillidae are free-living (Figure 33–1E) and have a distinct head, with simple four- or five-segmented antennae, chewing mouthparts, and compound eyes. The females of the parasitic species usually lack eyes, antennae, and legs; the body segmentation is very indistinct; and the head and thorax are fused (Figure 33–1G). The metamorphosis is complete.

The life history of the parasitic forms in this order is rather complex and involves hypermetamorphosis. A male, on emerging, seeks out and mates with a female, which never leaves its host. The female produces large numbers—up to several thousand—of tiny larvae, which escape from her body and the body of the host to the soil or to vegetation. These larvae, sometimes called *triungulins,* have well-developed eyes and legs (Figure 33–1F) and are fairly active insects. They locate and enter the body of the host. Once there, the larva molts into a legless, wormlike stage that feeds in the host's body cavity. After several molts, it pupates inside the last larval skin. The male, on emerging, leaves its host and flies about. The female remains in the host, with the anterior part of its body protruding between the abdominal segments of the host. After the young are produced, the female dies.

Species of Blattodea, Mantodea, Orthoptera, Hemiptera, Hymenoptera, and Thysanura are hosts of Strepsiptera. The host is not always killed, but it may be injured. The shape or color of the abdomen may be changed, or the sex organs may be damaged. The developing male strepsipteran usually causes more damage to its host than does the female.

Some entomologists (for example, Crowson 1960) place the Strepsiptera in the order Coleoptera (usually as a single family, the Stylopidae), largely because of the similarity in life history (hypermetamorphosis) between these insects and Meloidae and Rhipiphoridae. Most entomologists now recognize the group as a distinct order. However, their relationship to the other orders of insects is very controversial.

Until recently, most entomologists considered the Strepsiptera to be closely related to the Coleoptera. This conclusion was largely based on the fact that both orders use the hind wings to power their flight. Recent studies using characters from DNA sequences have postulated that the Strepsiptera in fact are most closely related to the Diptera (for example, see Whiting and Wheeler 1994, Wheeler et al. 2001). Whiting (1998) has reinterpreted the molecular and morphological evidence pertaining to the relationships of the order. This conclusion is not universally accepted, however. An alternative interpretation is that the perceived relationship to Diptera that emerges from a phylogenetic analysis is the result of methodological problems (long-branch attraction, see Carmean and Crespi 1995 and subsequent papers). At present, the strongest hypothesis seems to be the sister group relationship with Diptera.

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[1] Strepsiptera: *strepsi,* twisted; *ptera,* wings.

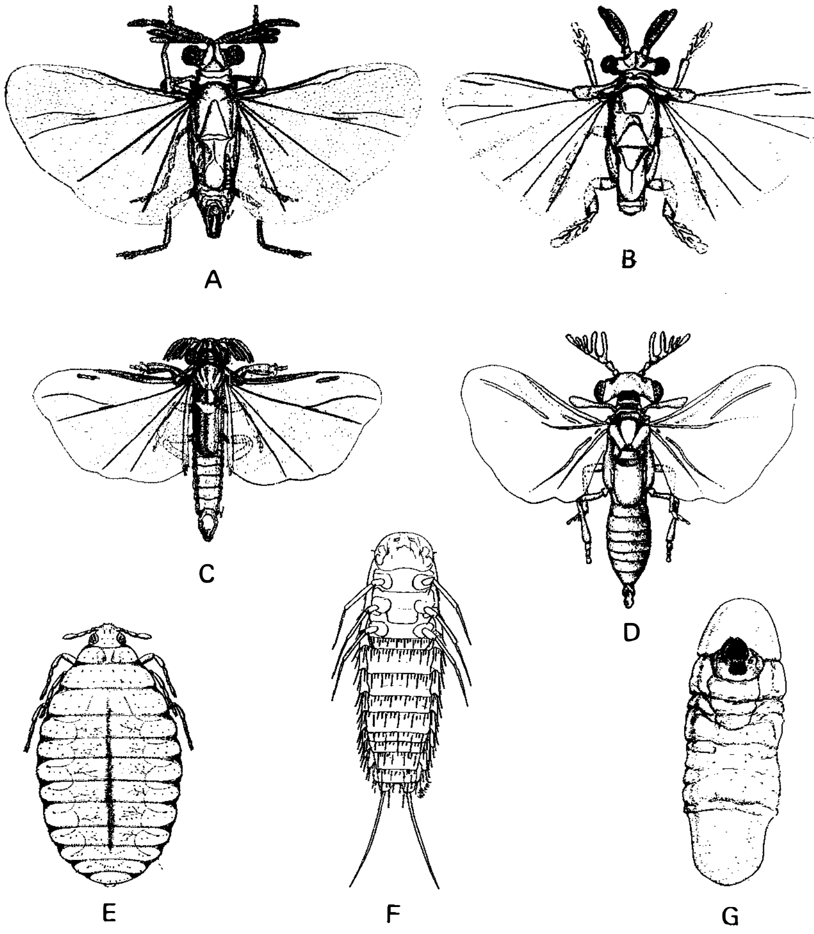


Figure 33–1 Strepsiptera. A, *Triozocera mexicana* Pierce (Corioxenidae), male; B, *Neostylops shannoni* Pierce (Stylopidae), male; C, *Halictophagus oncometopiae* (Pierce) (Halictophagidae), male; D, *Halictophagus serratus* Bohart (Halictophagidae); E, *Eoxenos laboulbenei* Peyerimhoff (Mengenillidae), female; F, *Stylops californica* Pierce (Stylopidae), triungulin, ventral view; G, *Halictophagus oncometopiae*, female, ventral view. (A–C, F, and G, courtesy of Pierce; D, courtesy of Bohart; E, courtesy of Parker and Smith; A–C, F–G, courtesy of the U.S. National Museum; D–E, courtesy of the Entomological Society of America.)

Key to the Families of Strepsiptera (Males)

1.	Tarsi 2-segmented; antenna 4-segmented, third segment with a long lateral process	Elenchidae	p. 671
1′.	Tarsi 3- to 5-segmented; antenna with 5–7 segments, lateral process present on third segment, often on additional segments beyond third	2	
2(1′).	Tarsi 3-segmented; antenna with 6–7 segments	Halictophagidae	p. 671
2′.	Tarsi 4- to 5-segmented; antenna with 4–7 segments	3	
3(2′).	Mandibles absent; tarsi 4- to 5-segmented	Corioxenidae	p. 671
3′.	Mandibles present; tarsi 4-segmented	4	
4(3′).	Antenna with 4–6 segments, segments broad and flat; parasitic on Hymenoptera (Apoidea, Sphecoidea, Vespoidea)	Stylopidae	p. 671
4′.	Antenna 7-segmented, segments narrow and round; parasitic on ants and, possibly, Orthoptera and Mantodea	Myrmecolacidae	p. 671

Family **Corioxenidae:** This family is represented in the United States by three species. *Triozocera mexicana* Pierce occurs in the southern states south into Brazil. It is a parasite of the cydnid *Pangaeus bilineatus* (Say). *Floridaxenos monroensis* Kathirithamby and Peck was recently described from Monroe County, Florida. *Loania canadensis* Kinzelbach, from Canada and the United States, parasitizes bugs in the family Cymidae (*Kleidocerys*).

Family **Elenchidae:** This group is represented by the widely distributed species *Elenchus koebelei* (Pierce), found in the southern United States. These insects are parasites of planthoppers (Delphacidae).

Family **Halictophagidae:** This is the second-largest family in the order, with about 14 North American species. Its members are parasites of leafhoppers, planthoppers, treehoppers, and pygmy mole crickets; species in other parts of the world parasitize cockroaches and flies.

Family **Myrmecolacidae:** This family is unique in that the two sexes attack different insect hosts: The males parasitize ants and the females develop in Orthoptera and Mantodea. Two species in the family have been recorded in the United States, *Caenocholax fenyesi* Pierce from the southern states (Florida west to Arizona), and *Stichotrema beckeri* (Oliveira and Kogan) from south Florida. *Caenocholax fenyesi* males parasitize the imported fire ant, *Solenopsis invicta* Buren.

Family **Stylopidae:** This is the largest family in the order, with 70 species in the United States and Canada. Most of its members are parasitic on bees (Andrenidae, Halictidae, and Hylaeinae), but some are parasitic on wasps (Polistinae, Eumeninae, and Sphecinae). The first-instar larvae of *Stylops pacifica* Bohart are transported from flowers to the nest of their host, *Andrena caerulea* Smith, within the crop of a foraging bee.

Collecting and Preserving Strepsiptera

The most satisfactory way to collect Strepsiptera is to collect parasitized hosts and to rear the parasites. Bees, wasps, leafhoppers, planthoppers, and other insects may harbor Strepsiptera. The parasitized hosts can often be recognized by the distorted abdomen, and one end of the parasite sometimes protrudes from between two of the abdominal segments. The males of some species are attracted to lights. Males of *Stylops* are attracted to virgin females in hosts (bees) that are placed in screen cages and can be collected on or flying about the cages (MacSwain 1949).

Strepsiptera should be preserved in alcohol and, for detailed study, should be mounted on microscope slides.

References

Bohart, R. M. 1941. A revision of the Strepsiptera with special reference to the species of North America. Calif. Univ. Publ. Entomol. 7(6):91–160.

Bohart, R. M. 1943. New species of *Halictophagus* with a key to the genus in North America (Strepsiptera, Halictophagidae). Ann. Entomol. Soc. Amer. 36:341–359.

Carmean, D., and B. J. Crespi. 1995. Do long branches attract flies? Nature 373: 234.

Crowson, R. A. 1960. The phylogeny of the Coleoptera. Annu. Rev. Entomol. 5:114–134.

Johnson, V. 1972. The female and host of *Triozocera mexicana* (Strepsiptera: Mengeidae). Ann. Entomol. Soc. Amer. 66:671–672.

Kathirithamby, J. 1989. Review of the order Strepsiptera. Syst. Entomol. 14:41–92.

Kathirithamby, J., and S. B. Peck. 1994. Strepsiptera of south Florida and the Bahamas with the description of a new genus and species of Corioxenidae. Can. Entomol. 126:125–134.

Kinzelbach, R. K. 1970. *Loania canadensis* n. gen. n. sp. und die Untergliederung der Callipharixenidae (Insecta: Strepsiptera). Senckenbergiana Biol. 51: 99–107.

Kinzelbach, R. K. 1971. Morphologische Befunde an Fächerfluglern und ihre phylogenetische Bedeutung (Insecta: Strepsiptera). Zoologica 119(1,2):1–256.

Kinzelbach, R. K. 1990. The systematic position of Strepsiptera (Insecta). Amer. Entomol. 36:292–303.

MacSwain, J. W. 1949. A method for collecting male *Stylops*. Pan-Pac. Entomol. 25:89–90.

Pierce, W. D. 1964. The Strepsiptera are a true order, unrelated to the Coleoptera. Ann. Entomol. Soc. Amer. 57:603–605.

Wheeler, W. C., M. Whiting, Q. D. Wheeler, and J. M. Carpenter. 2001. The phylogeny of the extant hexapod orders. Cladistics 71:113–169.

Whiting, M. F. 1998. Phylogenetic position of the Strepsiptera: Review of molecular and morphological evidence. Int. J. Insect Morphol. Embryol. 27:53–60.

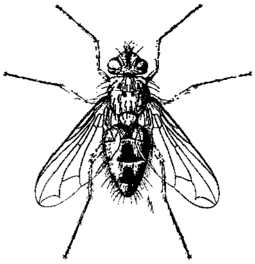
Whiting, M. F., and W. C. Wheeler. 1994. Insect homeotic transformation. Nature 368:696.

Whiting, M. F., J. M. Carpenter, Q. D. Wheeler, and W. C. Wheeler. 1997. The Strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Syst. Biol. 46:1–68.

34

Order Diptera[1]

Flies



The Diptera constitute one of the largest orders of insects, and its members are abundant in individuals and species almost everywhere. Most Diptera can be readily distinguished from other insects to which the term *fly* is applied (sawflies, stoneflies, caddisflies, dragonflies, and others) by the fact that they have one pair of wings, namely the front wings. The hind wings are reduced to small, knobbed structures called *halteres,* which function as organs of equilibrium. Occasionally insects in a few other orders have only one pair of wings (some mayflies, some beetles, male scale insects, and others), but none, except male scale insects, has the hind wings reduced to halteres. The Diptera are sometimes spoken of as "the two-winged flies," to distinguish them from the "flies" in other orders. In the common names of Diptera, we write the *fly* of the name as a separate word (for example, *fruit fly*), whereas in the common names of flies in other orders, we write the *fly* of the name together with the descriptive word (for example, *butterfly*).

The majority of the Diptera are relatively small and soft-bodied insects, and some are quite minute, but many are of great economic importance. On the one hand, for example, the mosquitoes, black flies, punkies, horse flies, stable flies, and others are bloodsucking and are serious pests of humans and animals. Many bloodsucking flies, and some scavenging flies, such as the house flies and blow flies, are important vectors of disease. The causative organisms of malaria, yellow fever, filariasis, dengue, sleeping sickness, typhoid fever, dysentery, and other diseases are carried and distributed by Diptera. Some flies, such as the Hessian fly and the apple maggot, are important pests of cultivated plants. On the other hand, many flies are useful as scavengers, others are important predators or parasites of various insect pests, others help pollinate useful plants, and some attack noxious weeds.

The mouthparts of Diptera are of the sucking type, but mouthpart structure varies considerably within the order. In many flies the mouthparts are piercing; in others they are sponging or lapping; and in a few flies, the mouthparts are so poorly developed as to be nonfunctional.

The Diptera undergo complete metamorphosis, and the larvae of many are called *maggots.* The larvae are generally legless and wormlike. In the basal families in the Nematocera, the head is usually well developed and the mandibles move laterally. In the more derived families (Brachycera), the head is reduced and the mouth hooks move in a vertical plane. In some families of Brachycera, the head of the larva is sclerotized and more or less retractile, whereas others have no sclerotization of the head at all except for the mouthparts. The pupae of the Nematocera are of the obtect type, whereas those of other Diptera are coarctate; that is, the pupal stage is passed inside the last larval cuticle, which is called a *puparium.*

Dipterous larvae live in many kinds of habitats, but a large proportion live in water—in all sorts of aquatic habitats including streams, ponds, lakes, temporary puddles, and brackish and alkaline water. The larvae that feed on plants generally live within some tissue of the plant, as leaf miners, gall insects, stem borers, or root borers. The predaceous larvae live in many different habitats: in water, in the soil, under bark or stones, or on vegetation. Many species feed during the larval stage in decaying plant or animal matter. Some fly larvae live in some rather unusual habitats: one species, *Helaeomyia petrolei* (Coquillett) (fam-

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[1] Diptera: *di,* two; *ptera,* wings.

ily Ephydridae), lives in pools of crude petroleum. Other ephydrids breed in the Great Salt Lake.

Adult Diptera feed on various plant or animal juices, such as nectar, sap, or blood. Most species feed on nectar, but many are bloodsucking, and many are predaceous on other insects.

Classification of the Diptera

Investigation of the phylogenetic relationships within the order Diptera is a particularly active and dynamic area. Entomological understanding of interrelationships is rapidly improving and, as a result, the formal classification is also quite dynamic. A recent summary of the state of knowledge can be found in Yeates and Wiegmann (1999). We now have strong evidence that a number of the groups traditionally recognized (such as Nematocera), are paraphyletic. Within the Brachycera, some monophyletic taxa are well established, but many questions remain. At this point, it is not possible to consistently apply formal taxonomic ranks within the order and still reasonably represent what consensus does exist among specialists. Therefore, we present the classification as an indented listing of families, but largely omit indication of the formal rank that each grouping occupies in a Linnaean hierarchy. Groups marked with an asterisk (*) are relatively rare or are unlikely to be taken by a general collector.

- Suborder Nematocera (Nemocera; Orthorrhapha in part)—long-horned flies
  - Tipulomorpha
    - Tipulidae (including Limoniidae, Cylindrotomidae)—crane flies
    - Trichoceridae (Trichoceratidae, Petauristidae)—winter crane flies*
  - Psychodomorpha
    - Psychodidae—moth flies and sand flies
  - Ptychopteromorpha
    - Ptychopteridae (Liriopeidae)—phantom crane flies
    - Tanyderidae—primitive crane flies*
  - Culicomorpha
    - Ceratopogonidae (Heleidae)—biting midges, punkies, no-see-ums
    - Chaoboridae (Culicidae in part)—phantom midges
    - Corethrellidae (Corethridae)
    - Chironomidae (Tendipedidae)—midges
    - Culicidae—mosquitoes
    - Dixidae (Culicidae in part)
    - Simuliidae (Melusinidae)—black flies or buffalo gnats
    - Thaumaleidae (Orphnephilidae)—solitary midges*
  - Blephariceromorpha
    - Blephariceridae (Blepharoceridae, Blepharoceratidae)—net-winged midges*
    - Deuterophlebiidae—mountain midges*
    - Nymphomyiidae*
  - Bibionomorpha
    - Anisopodidae (Rhyphidae, Silvicolidae, Phryneidae; including Mycetobiidae)—wood gnats
    - Axymyiidae (Pachyneuridae in part)
    - Bibionidae (including Hesperinidae)—march flies
    - Canthyloscelididae (Synneuridae, Hyperoscelididae)*
    - Cecidomyiidae (Cecidomyidae, Itonididae)—gall midges or gall gnats
    - Mycetophilidae (Fungivoridae in part, including Ditomyiidae, Diadociddidae, Keroplatidae, Lygistorrhinidae)—fungus gnats
    - Pachyneuridae (Cramptonomyiidae)*
    - Scatopsidae—minute black scavenger flies
    - Sciaridae (Fungivoridae in part)—dark-winged fungus gnats, root gnats
- Suborder Brachycera (including Cyclorrhapha and Orthorrhapha in part)—short-horned flies
  - Xylophagomorpha
    - Xylophagidae (Erinnidae; Rhagionidae in part)
  - Stratiomyomorpha
    - Stratiomyidae (Stratiomyiidae; including Chiromyzidae)—soldier flies
    - Xylomyidae (Xylomyiidae; Xylophagidae in part)
  - Tabanomorpha (Orthorrhapha in part)
    - Athericidae (Rhagionidae in part)
    - Pelecorhynchidae (Tabanidae in part, Xylophagidae in part)*
    - Rhagionidae (Leptidae)—snipe flies
    - Tabanidae—horse flies and deer flies
    - Vermileonidae (Rhagionidae in part)—worm lions*
  - Muscomorpha
    - Nemestrinioidea
      - Acroceridae (Acroceratidae, Cyrtidae, Henopidae, Oncodidae)—small-headed flies*
      - Nemestrinidae—tangle-veined flies*
    - Asiloidea
      - Apioceridae (Apioceratidae)—flower-loving flies*
      - Asilidae (including Leptogastridae)—robber flies and grass flies
      - Bombyliidae—bee flies
      - Hilarimorphidae (Rhagionidae in part)*

  - Mydidae (Mydaidae, Mydasidae)—mydas flies
  - Scenopinidae (Omphralidae)—window flies*
  - Therevidae—stiletto flies
- Empidoidea
  - Empididae (Empidae)—dance flies
  - Dolichopodidae (Dolochopidae)—long-legged flies
- Cyclorrhapha—circular-seamed flies
  - Aschiza
    - Lonchopteridae (Musidoridae)—spear-winged flies
    - Phoridae—humpbacked flies
    - Pipunculidae (Dorilaidae, Dorylaidae)—big-headed flies
    - Platypezidae (Clythiidae)—flat-footed flies*
    - Syrphidae—syrphid flies or flower flies
  - Calypteratae (Calyptratae)—calyptrate muscoid flies
  - Anthomyiidae (Anthomyidae; Muscidae in part)
  - Calliphoridae (Metopiidae in part)—blow flies
  - Fanniidae (Muscidae in part)
  - Hippoboscidae (Pupipara in part, Nycteribiidae, Streblidae)—louse flies, bat flies*
  - Muscidae—muscid flies: house fly, face fly, horn fly, stable fly, tsetse flies, and others
  - Oestridae (including Cuterebridae, Gasterophilidae, and Hypodermatidae)—warble flies and bot flies*
  - Rhinophoridae (Tachinidae in part)
  - Sarcophagidae (Stephanosomatidae; Metopiidae in part)—flesh flies
  - Scathophagidae (Scatophagidae, Scatomyzidae, Scopeumatidae, Cordyluridae, Anthomyiidae in part)—dung flies
  - Tachinidae (Larvaevoridae; including Phasiidae = Gymnosomatidae, and Dexiidae)
- Acalyptratae—acalyptrate muscoid flies
  - Superfamily Nerioidea
    - Micropezidae (including Tylidae and Calobatidae = Trepidariidae)—stilt-legged flies
    - Neriidae—cactus flies*
    - Pseudopomyzidae*
  - Superfamily Diopsoidea
    - Diopsidae—stalked-eyed flies*
    - Psilidae—rust flies
    - Tanypezidae (Micropezidae in part, Psilidae in part, including Strongylophthalmyiidae)
  - Superfamily Conopoidea
    - Conopidae—thick-headed flies
  - Superfamily Tephritoidea
    - Lonchaeidae (Sapromyzidae in part)
    - Pallopteridae (Sapromyzidae in part)—flutter flies
    - Piophilidae (including Neottiophilidae)—skipper flies
    - Pyrgotidae*
    - Richardiidae (Otitidae in part, including Thyreophoridae)*
    - Tephritidae (Trypetidae, Trupaneidae, Trypaneidae, Euribiidae)—fruit flies
    - Ulidiidae (Otitidae, Ortalidae, Ortalididae)—picture-winged flies
    - Platystomatidae (Otitidae in part)—picture-winged flies
  - Superfamily Lauxanioidea
    - Chamaemyiidae (Chamaemyidae, Ochthiphilidae)—aphid flies
    - Lauxaniidae (Sapromyzidae)
  - Superfamily Sciomyzoidea
    - Coelopidae (Phycodromidae)—seaweed flies
    - Dryomyzidae (including Helcomyzidae)*
    - Ropalomeridae (Rhopalomeridae)*
    - Sciomyzidae (Tetanoceridae, Tetanoceratidae)—marsh flies
    - Sepsidae—black scavenger flies
  - Superfamily Opomyzoidea
    - Acartophthalmidae (Clusiidae in part)
    - Agromyzidae (Phytomyzidae)—leaf-miner flies
    - Anthomyzidae (Opomyzidae in part)
    - Asteiidae (Astiidae)
    - Aulacigastridae (Aulacigasteridae; Anthomyzidae in part; Drosophilidae in part)*
    - Clusiidae (Clusiodidae, Heteroneuridae)
    - Odiniidae (Odinidae, Agromyzidae in part)
    - Opomyzidae (Geomyzidae)*
    - Periscelididae (Periscelidae)*
  - Superfamily Carnoidea
    - Braulidae (Pupipara in part)—bee lice
    - Canacidae (Canaceidae)—beach flies*
    - Carnidae (Milichiidae in part)*
    - Chloropidae (Oscinidae, Titaniidae)—grass flies
    - Cryptochetidae (Chamaemyiidae in part, Agromyzidae in part)*
    - Milichiidae (Phyllomyzidae)
    - Tethinidae (Opomyzidae in part)*
  - Superfamily Sphaeroceroidea
    - Chyromyidae (Chyromyiidae)

Heleomyzidae (Helomyzidae, including Trixoscelididae, Rhinotoridae)
Sphaeroceridae (Sphaeroceratidae, Borboridae, Cypselidae)—small dung flies
Superfamily Ephydroidea
Camillidae (Drosophilidae in part)*
Curtonotidae (Cyrtonotidae; Drosophilidae in part)
Diastatidae (Drosophilidae in part)*
Drosophilidae—pomace flies, vinegar flies, small fruit flies
Ephydridae (Hydrellidae, Notiophilidae)—shore flies

Characters Used in Identifying Diptera

The principal characters used in identifying the Diptera are those of the antennae, legs, wings, and chaetotaxy (the arrangement of the bristles, chiefly of the head and thorax). Occasionally various other characters are used, such as those of the head, and the size, shape, and color of the insect.

Antennae

The antennae vary quite a bit from family to family, and to some extent within a single family. Occasionally they differ in the two sexes of the same species (for example, mosquitoes; see Figure 34–36). Basically, the antennae of a fly consist of three segments: the scape (the basal segment), pedicel, and flagellum. In the Nematocera the flagellum is divided into four or more distinct and movable subdivisions (which we call *segments,* but which are sometimes called *flagellomeres*). In some of the Brachycera, the third antennal segment is subdivided, but the divisions are not as distinct as those between the three basic segments, and such a segment is said to be "annulated" (Figure 34–1C,D,F). This annulation is sometimes difficult to see unless the antenna is properly illuminated. In a few cases it can be difficult to decide whether such an antenna is three-segmented or many-segmented. The third antennal segment in many Brachycera bears an elongate process: a style or an arista. A style is usually terminal and fairly rigid, whereas an arista is usually dorsal and is bristlelike. Both styles and aristae can appear segmented, although the segments (particularly in an arista) are often difficult to see. An arista can be bare, pubescent, or plumose. In some of the Muscomorpha, the form of the second antennal segment can serve to separate different groups; for example, the calyptrate and acalyptrate groups of muscoid flies differ in the form of the second antennal segment (Figure 34–19A,B).

Legs

The principal leg characters used in separating groups of flies are the structure of the empodium, the presence or absence of tibial spurs, and the presence of certain tibial bristles. The empodium (Figure 34–2, *emp*) is a

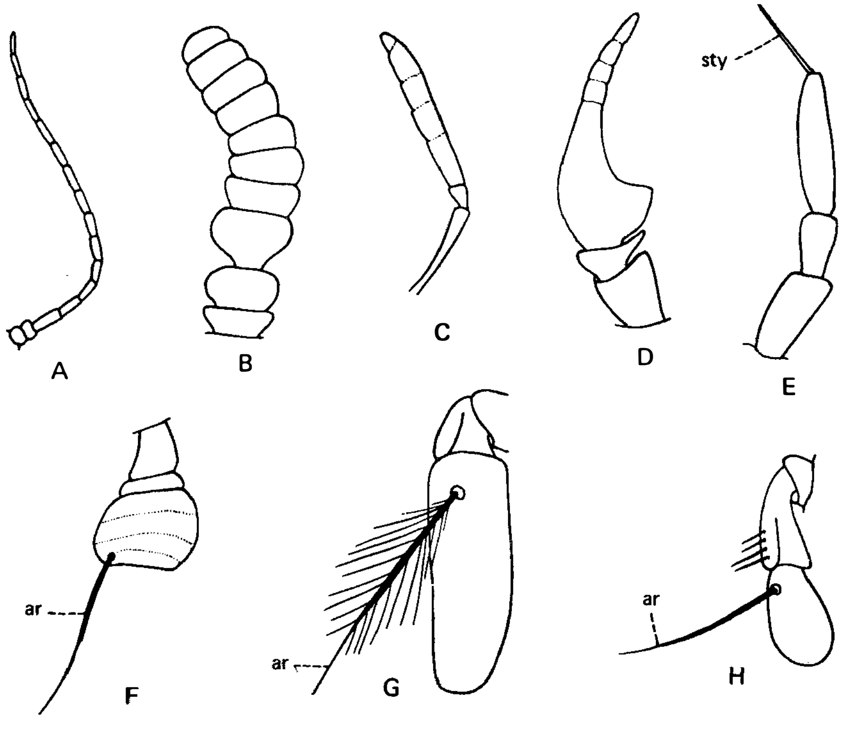

Figure 34–1 Antennae of Diptera. A, Mycetophilidae (*Mycomyia*); B, Bibionidae (*Bibio*); C, Stratiomyidae (*Stratiomys*); D, Tabanidae (*Tabanus*); E, Asilidae (*Asilus*); F, Stratiomyidae (*Ptecticus*); G, Calliphoridae (*Calliphora*); H, Tachinidae (*Epalpus*). *ar*, arista; *sty*, style.

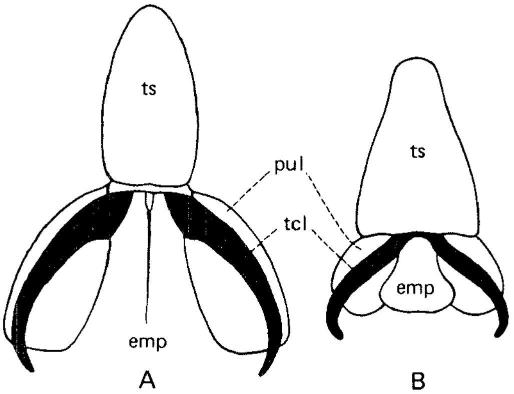

Figure 34–2 Tip of tarsus, dorsal view. **A**, robber fly, with the empodium bristlelike; **B**, horse fly, with the empodium pulvilliform. *emp*, empodium; *pul*, pulvilli; *tcl*, tarsal claw; *ts*, last tarsal segment.

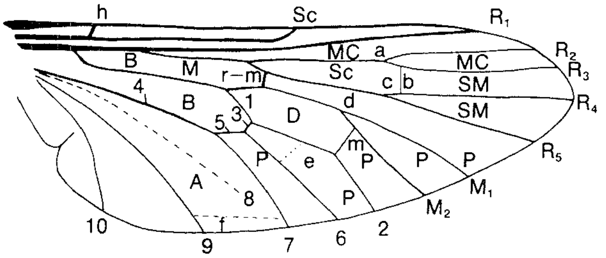

Figure 34–3 Generalized dipteran venation (Comstock-Needham terminology for the veins), with a comparison of the major interpretations of the veins behind M_2. *A*, anal cell; *B*, basal cells; *D*, discal cell; *MC*, marginal cells; *P*, posterior cells; *SM*, submarginal cells.

Interpretations of the Veins behind M_2

Vein Number	Comstock[a]	Tillyard[b]	McAlpine[c]
1	M_3	M_{3+4}	M_3
2	M_3	M_3	M_3
3	m-cu	M_4	m-cu
4	Cu	Cu_1	CuA
5	Cu_1	M_4	CuA_1
6	Cu_1	M_4	CuA_1
7	Cu_2	Cu_1	CuA_2
8[d]	1A	Cu_2	CuP
9	2A	1A	A_1
10	3A	2A	A_2

[a] The terminology used in this book (from Comstock, J. H., 1940).

[b] Tillyard, R. J., 1926.

[c] McAlpine et al., 1981. In wings where the M_3 of Comstock fuses with the Cu_1 of Comstock, these authors do not recognize an M_3; if M_{1+2} is forked they call its branches M_1 and M_2, but if it is not forked they call it M (see Figure 34–4).

[d] Nearly always weak, often completely absent.

structure arising from between the claws on the last tarsal segment. It is bristlelike or absent in most flies, but in a few families (Figure 34–2B) it is large and membranous and resembles the pulvilli in appearance. The pulvilli are pads at the apex of the last tarsal segment, one at the base of each claw (Figure 34–2, *pul*). A fly can thus have two pads (the pulvilli), three pads (the pulvilli and a pulvilliform empodium), or no pads (pulvilli absent) on the last tarsal segment. Tibial spurs are spinelike structures, usually located at the distal end of the tibia. Preapical tibial bristles are bristles on the outer or dorsal surface of the tibia just proximad of the apex (Figure 34–26B, *ptbr*).

Wings

Entomologists make considerable use of wing characters, especially venation, in identifying flies, and it is often possible to identify a fly to family or beyond by wings alone. Venation in this order is relatively simple, and many families tend toward reduction in number of veins. Sometimes the wing's color, its shape, or character of the lobes at the wing base is useful in identification.

In most fly wings there is an incision on the posterior side of the wing near the base that separates off a small basal lobe, called the *alula*. Distal to the alula is the anal angle of the wing, and the lobe there is called the *anal lobe* (Figure 34–4C, al). At the extreme base of the wing, basad of the alula, there are often two lobes called the *calypteres* (singular, *calypter*). The one next to the alula is the upper calypter, and the other one the lower calypter. The calypteres can vary in size or shape in different groups.

Two different venational terminologies are commonly used in this order, that of Comstock-Needham and an older system in which the principal longitudinal veins are numbered. Most authorities use the Comstock-Needham terminology, but not all agree with the Comstock-Needham interpretation, particularly regarding the veins posterior to M_2. Figure 34–3 shows a generalized dipteran wing, labeled with the Comstock-Needham terminology through M_2 and comparing three major interpretations of the veins posterior to M_2. We follow the Comstock-Needham interpretation in this book, but occasionally use terms of the older system, especially for certain wing cells. Table 34–1 compares the different venational terminologies used for dipteran wing venation, and Figure 34–4 shows some dipteran wings labeled with these terminologies.

A closed cell is one that does not reach the wing margin (for example, the anal or 1A cell in Figure 34–4A, B). When the thickening of the anterior edge of the wing (the costa) ends near the wing tip

Table 34–1 A Comparison of Diptera Venational Terminologies

Comstock	Tillyard (1926)	McAlpine *et al.* (1981)	Old System
Veins			
C	C	C	Costal
Sc	Sc	Sc	Auxiliary
R$_1$	R$_1$	R$_1$	First longitudinal
R$_{2+3}$	R$_{2+3}$	R$_{2+3}$	Second longitudinal
R$_{4+5}$	R$_{4+5}$	R$_{4+5}$	Third longitudinal
M$_{1+2}$	M$_{1+2}$	M$_{1+2}$ or M[a]	Fourth longitudinal
m-cu	base of M$_4$	m-cu	Discal cross vein
Cu	Cu	CuA	Fifth longitudinal
base of Cu$_1$	m-cu	base of CuA$_1$	Fifth longitudinal
Cu$_1$	M$_4$	CuA$_1$	Fifth longitudinal
Cu$_2$	Cu$_1$	CuA$_2$	Fifth longitudinal
1A[b]	Cu$_2$	CuP	—
2A	1A	A$_1$	Sixth longitudinal
H	h	h	Humeral cross vein
r-m	r-m	r-m	Anterior cross vein
M	m	m-m	Posterior cross vein
M$_3$	M$_{3+4}$ and M$_3$	M$_3$	Fifth longitudinal
Cells			
C	C	c	Costal
Sc	Sc	sc	Subcostal
R	R	br[c]	First basal
M	M	bm[d]	Second basal
R$_1$, R$_2$	R$_1$, R$_2$	r$_1$, r$_2$	Marginal
R$_3$	R$_3$	r$_3$, r$_{2+3}$[e]	First submarginal
R$_4$	R$_4$	r$_4$	Second submarginal
R$_5$	R$_5$	r$_5$, r$_{4+5}$[f]	First posterior
M$_1$	M$_1$	m$_1$	Second posterior
1st M$_2$	1st M$_2$	d (discal)	Discal
2nd M$_2$	2nd M$_2$	m$_2$	Third posterior
M$_3$	M$_3$	M$_3$	Fourth posterior
Cu$_1$	M$_4$	cua$_1$	Fifth posterior
1A	Cu$_2$	cup	Anal
2A	1A	a$_1$	Axillary

[a] When no M$_3$ is recognized and this vein is not forked.

[b] Usually weak, often lacking.

[c] Basal radial cell.

[d] Basal medial cell.

[e] When R$_{2+3}$ is not forked.

[f] When R$_{4+5}$ is not forked.

(as in Figure 34–8B–FJ), the costa is said to extend only to the wing tip. Where there is no abrupt thinning of the anterior margin of the wing near the wing tip (as in Figure 34–8G–I), the costa is said to continue around the wing.

Many muscoid flies have one or two points in the costa where sclerotization is weak or lacking, or where the vein appears broken. Such points *costal breaks* can occur near the end of R$_1$ or the humeral crossvein (Figures 34–22B and 34–24C–E, *cbr*). Costal breaks are best seen with transmitted light. A few muscoids have a series of long hairs or bristles along the costa beyond the end of R$_1$ (Figure 34–22A,H). The costa in such cases is said to be *spinose*.

Chaetotaxy

In identifying certain flies, particularly the muscoid groups, much use is made of the number, size, position, and arrangement of the larger bristles on head

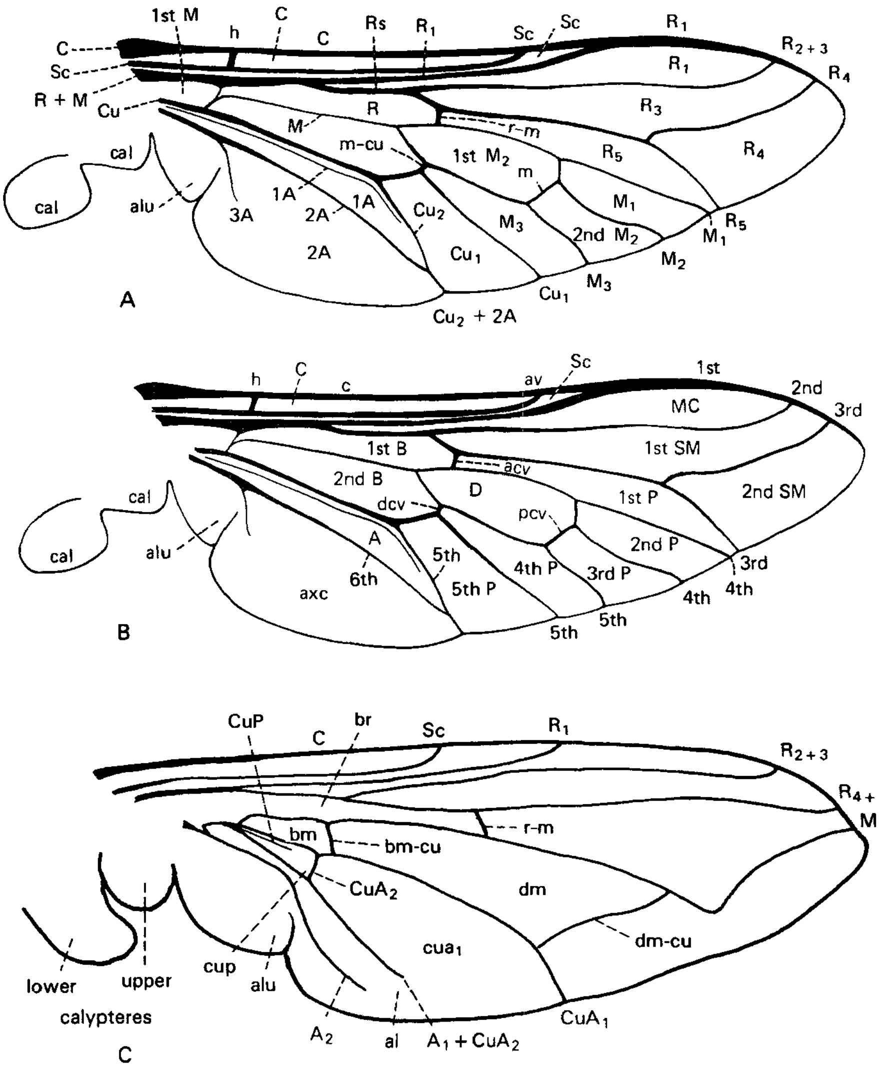

Figure 34–4 Wings of a horse fly (A and B) and a calyptrate muscoid fly (C), showing venational terminologies. A, Comstock-Needham system; B, an older system, in which the longitudinal veins are numbered; C, the terminology used by McAlpine et al. (1981). For a key to the lettering in A and the longitudinal veins in C, see Chapter 2. Labeling in B: *A*, anal cell; *acv*, anterior cross vein; *alu*, alula; *av*, auxiliary vein; *axc*, axillary cell; *B*, basal cells (first and second); *C*, costal cell; *c*, costal vein; *cal*, calypteres or squamae; *D*, discal cell; *dcv*, discal crossvein; *h*, humeral crossvein; *MC*, marginal cell; *P*, posterior cells; *pcv*, posterior crossvein; *Sc*, subcostal cell; *SM*, submarginal or apical cells (first and second). Labeling in C: *al*, anal lobe; *alu*, alula; *bm*, basal medial cell; *bm-cu*, basal mediocubital crossvein; *br*, basal radial cell; *cua*$_1$, anterior cubital cell; *cup*, posterior cubital cell; *dm*, discal medial cell; *dm-cu*, discal mediocubital crossvein.

and thorax. The terminology used in the chaetotaxy of flies is illustrated in Figures 34–5 and 34–6. The frontal bristles (not shown in Figure 34–5) are in the middle of the front, between the ocellar triangle and the frontal suture.

Head and Thoracic Sutures

The principal head suture used in identifying flies is the frontal suture (Figure 34–5, fs). This suture is usually in the shape of an inverted U, extending from above the bases of the antennae lateroventrad toward

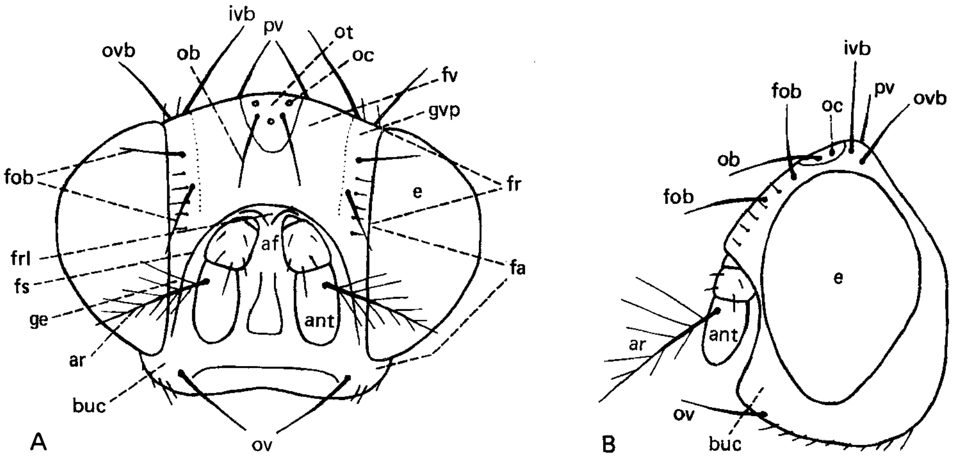

Figure 34–5 Areas and chaetotaxy of the head of a drosophilid fly. A, anterior view; B, lateral view. *af*, antennal fossa; *ant*, antenna; *ar*, arista; *buc*, bucca; *e*, compound eye; *fa*, face; *fob*, fronto-orbital bristles; *fr*, frons; *frl*, frontal lunule; *fs*, frontal suture; *fv*, frontal vitta; *ge*, gena; *gvp*, genovertical or orbital plate; *ivb*, inner vertical bristle; *ob*, ocellar bristle; *oc*, ocellus; *ot*, ocellar triangle; *ov*, oral vibrissae; *ovb*, outer vertical bristle; *pv*, postvertical bristles.

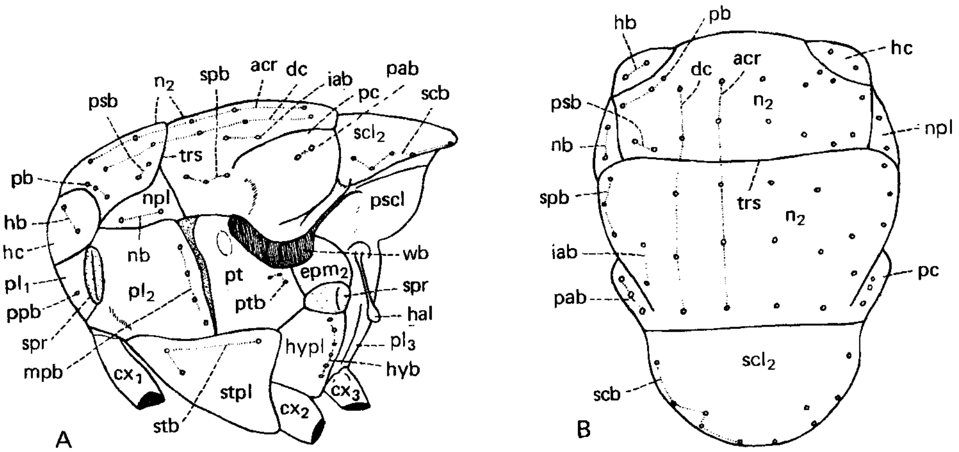

Figure 34–6 Areas and chaetotaxy of the thorax of a blow fly. A, lateral view; B, dorsal view. *acr*, acrostichal bristles; *cx*, coxa; *dc*, dorsocentral bristles; epm_2, mesepimeron; *hal*, haltere; *hb*, humeral bristles; *hc*, humeral callus; *hyb*, hypopleural bristles; *hypl*, hypopleuron; *iab*, intra-alar bristles; *mpb*, mesopleural bristles; n_2, mesonotum; *nb*, notopleural bristles; *npl*, notopleuron; *pab*, postalar bristles; *pb*, posthumeral bristles; *pc*, postalar callus; pl_1, propleuron; pl_2, mesopleuron; pl_3, metapleuron; *ppb*, propleural bristle; *psb*, presutural bristles; *pscl*, postscutellum; *pt*, pteropleuron; *ptb*, pteropleural bristles; *scb*, scutellar bristles; scl_2, mesoscutellum; *spb*, supra-alar bristles; *spr*, spiracle; *stb*, sternopleural bristles; *stpl*, sternopleuron; *trs*, transverse suture; *wb*, base of wing.

Table 34–2 Comparison of Terminologies of Thoracic Areas

This Book		McAlpine *et al.* (1981)	
Symbol	Name of Area	Symbol	Name of Area
hc	humeral callus	ppn	postpronotum
npl	notopleuron	npl	notopleuron
pscl	postscutellum	sbsctl	subscutellum
pl_1	propleuron	prepm	proepimeron
pl_2	mesopleuron	anepst	anepisternum
pt	pteropleuron	anepm	anepimeron
stpl	sternopleuron	kepst	katepisternum
hypl	hypopleuron	mr	meron
epm_2	mesepimeron	ktg	katatergite

the lower margins of the compound eyes. Dipterists commonly call this the *frontal suture*, but it is not the same as the frontal sutures in Figure 2–13. It is actually a ptilinal suture and marks the break in the head wall through which the ptilinum was everted at the time of the fly's emergence from the puparium.

Between the apex of the U and the bases of the antennae is a small, crescent-shaped sclerite called the *frontal lunule* (*frl*). The presence of a frontal suture distinguishes the muscoid flies from others. In cases where the complete suture is difficult to see, flies having it can be recognized by the presence of a frontal lunule above the bases of the antennae.

A transverse suture across the anterior part of the mesonotum (Figure 34–6, *trs*) separates most of the calyptrate from the acalyptrate muscoids. The calyptrate muscoids usually have sutures in the lateroposterior portions of the mesonotum, which separate the postalar calli (Figure 34–6, *pc*). The acalyptrate muscoids lack these sutures.

The terms used by McAlpine et al. (1981) for the various thoracic areas are for the most part different from the terms we use. Hence their terms for most of the thoracic bristles are a little different from ours. A comparison of these two terminologies is given in Table 34–2.

Size

In the keys and descriptions in this chapter, "medium-sized" means about the size of a house fly or a blue-bottle fly. "Small" means smaller, and "large" means larger than this size. "Very small" or "minute" means less than 3 mm long, and "very large" means 25 mm or more.

Key to the Families of Diptera

Some difficulty may be encountered with small or minute specimens, and a microscope with considerable magnification (90 to 120×) may be necessary for examining such specimens. Acalyptrate muscoids (which key out from couplet 76) in which the head or the thoracic bristles are broken off or embedded in glue (specimens on a point) can be difficult or impossible to run through the key.

In the following key, families marked with an asterisk (*) are relatively rare or are unlikely to be taken by a general collector. Keys to larvae can be found in McAlpine et al. (1981).

1.	Wings present and well developed, longer than thorax	2	
1′.	Wings greatly reduced, usually shorter than thorax, or absent	141*	
2(1).	Wings extremely narrow, pointed apically, with greatly reduced venation and no closed cells, with a very long fringe; antennal flagellum elongate, annulated basally, clubbed; eyes separated dorsally but contiguous ventrally; small, aquatic flies, less than 2 mm long, slender, pale, weakly sclerotized; found in rapid streams in Quebec, New Brunswick, and the Appalachian Mountains south to Alabama	Nymphomyiidae*	p. 715
2′.	Without the preceding combination of characters	3	
3(2′).	Antennae of 6 or more freely articulated segments (Figure 34–1A,B), in some males very long and plumose (Figure 34–36B,D); Rs 1–4 branched, if 3-branched, it is nearly always R_{2+3} that is forked; palps usually with 3–5 segments (suborder Nematocera)	4	

3′.	Antennae of 5 or fewer (usually 3) segments, third segment sometimes annulated (appearing divided into subsegments, but not as distinct as the 3 main antennal segments), often bearing a terminal or dorsal style or arista (Figure 34–1C–H), never long and plumose: Rs 2- or 3-branched (rarely unbranched), if 3-branched it is nearly always R_{4+5} that is forked; palps with not more than 2 segments (suborder Brachycera)	31	
4(3).	Mesonotum with V-shaped suture; legs long and slender (Figure 3434–28A)	5	
4′.	Mesonotum without V-shaped suture; legs variable	8	
5(4).	Ocelli present; V-shaped suture on mesonotum incompletely developed in middle; 3A short, half as long as 2A or shorter, and curved	Trichoceridae*	p. 707
5′.	Ocelli absent; V-shaped suture on mesonotum complete; 3A usually more than half as long as 2A and relatively straight, or absent	6	
6(5′).	R 5-branched, all 5 branches reaching wing margin; M_3 cell sometimes (*Protoplasa*, Figure 34–7E) with a crossvein; 3A absent	Tanyderidae*	p. 708
6′.	R with 4 or fewer branches reaching wing margin; M_3 cell without a crossvein; 3A present or absent	7	
7(6′).	Only 1 anal vein (2A) reaching wing margin (3A absent), and no closed discal cell (Figure 34–7A); halteres with small process at base	Ptychopteridae	p. 708

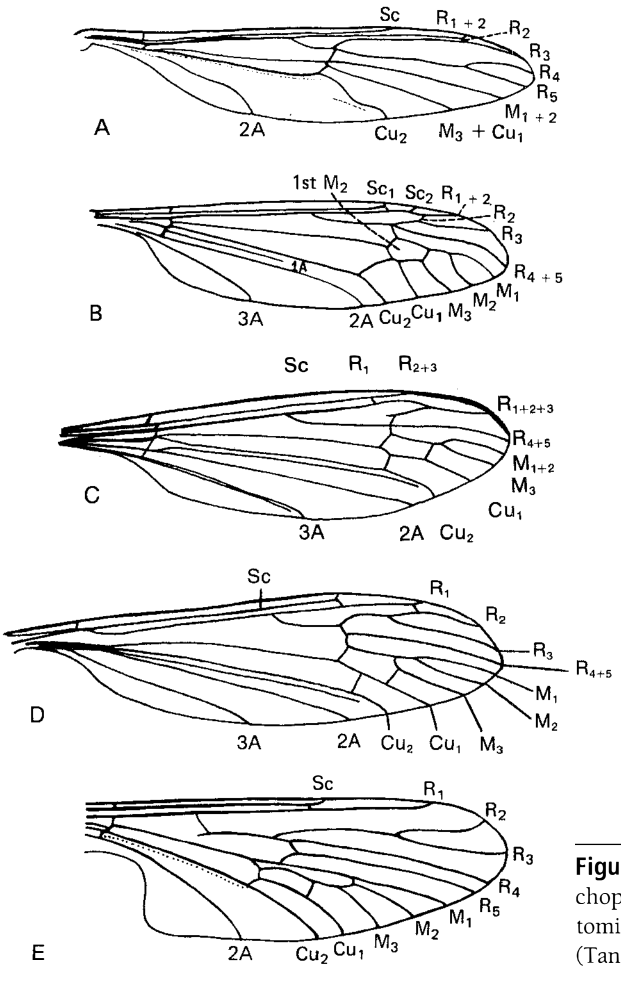

Figure 34–7 Wings of crane flies. A, *Bittacomorpha* (Ptychopteridae); B, *Tipula* (Tipulidae, Tipulinae); C, Cylindrotominae (Tipulidae); D, Limoniinae (Tipulidae); E, *Protoplasa* (Tanyderidae).

7′.	Two anal veins reaching wing margin (3A present); R 2- to 4-branched, closed discal cell usually present (Figure 34–7B–D); halteres without a process at base	Tipulidae	p. 707
8(4′).	Wings broad, broadest in basal fourth, venation reduced and a fanlike development of folds present; antennae very long in male, at least 3 times as long as body, 6-segmented; ocelli and mouthparts absent; western United States	Deuterophlebiidae*	p. 715
8′.	Without the preceding combination of characters	9	
9(8′).	Ocelli present	10	
9′.	Ocelli absent	22	
10(9).	A closed discal cell present	11	
10′.	No closed discal cell present	13	
11(10).	Fourth posterior (M_3) cell open	12	
11′.	Fourth posterior cell closed; medium-sized, elongate flies resembling sawflies (*Rachicerus*)	Xylophagidae*	p. 719
12(11).	The two branches of Rs connected by a crossvein; western North America, Oregon to British Columbia	Pachyneuridae*	p. 718
12′.	The two branches of Rs not connected by a crossvein (Figure 34–8B); widely distributed	Anisopodidae (Anisopodinae)	p. 715
13(10′).	Venation reduced, with 6 or fewer longitudinal veins (Figures 34–8A,E; 34–9B; 34–10C,D)	14	
13′.	Venation not so reduced, with 7 or more longitudinal veins (Figures 34–8C,J, 34–9C, 34–10A,B)	18	
14(13).	Tibial spurs present; eyes meeting above bases of antennae (except in males of *Pnyxia*, in which the eyes are reduced); antennae 16-segmented, usually about as long as head and thorax combined; C ending at wing tip, Rs unbranched, r-m in line with Rs (Figure 34–10C,D)	Sciaridae	p. 718
14′.	Tibial spurs absent; antennae with 15 or fewer segments; other characters variable	15	
15(14′).	Antennae relatively short and thick, only a little longer than head; C ending before wing tip	16	
15′.	Antennae longer and slender; C variable	17	
16(15).	Palps 1-segmented; antennae with 12 or fewer segments; C ending at one half to three fourths the wing length (Figure 34–9B); eyes well separated below antennae; common insects, widely distributed	Scatopsidae	p. 718
16′.	Palps 4-segmented; antennae with 12–16 segments; C ending near wing tip; eyes narrowly separated to nearly contiguous ventrally; rare insects, known from Quebec to California, north to Alaska	Canthyloscelididae*	p. 716
17(15′).	Antennae as long as or longer than head and thorax combined; C usually continuing around wing tip though weaker behind; long-legged, rather delicate flies	Cecidomyiidae (Lestremiinae)	p. 716
17′.	Antennae usually shorter than head and thorax combined; C usually ending at wing tip; body shape variable	Ceratopogonidae	p. 708
18(13′).	Legs long and slender, insect resembling a crane fly; anal angle of wing projecting (Figure 34–8J); wings sometimes with a network of fine lines between veins	Blephariceridae*	p. 714
18′.	Without the preceding combination of characters	19	
19(18′).	Tibial spurs present; Rs simple or 2-branched	20	

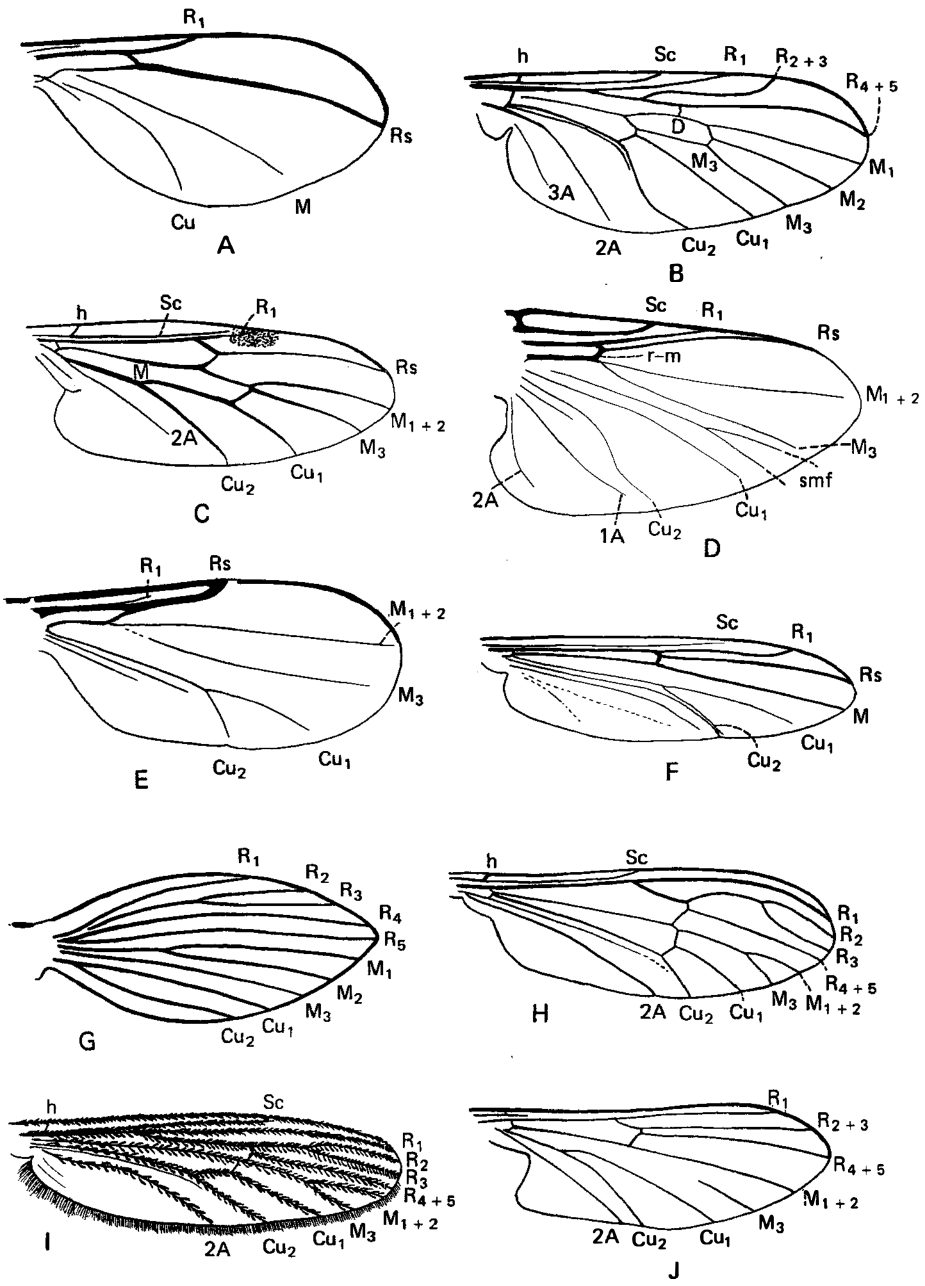

Figure 34–8 Wings of Nematocera. A, Cecidomyiidae; **B**, Anisopodidae (*Silvicola*); C, Bibionidae (*Bibio*); **D**, Simuliidae (*Simulium*); **E**, Ceratopogonidae; F, Chironomidae; G, Psychodidae (*Psychoda*); **H**, Dixidae (*Dixa*); I, Culicidae (*Psorophora*); J, Blephariceridae (*Blepharicera*). *D*, discal cell; *smf*, submedian fold.

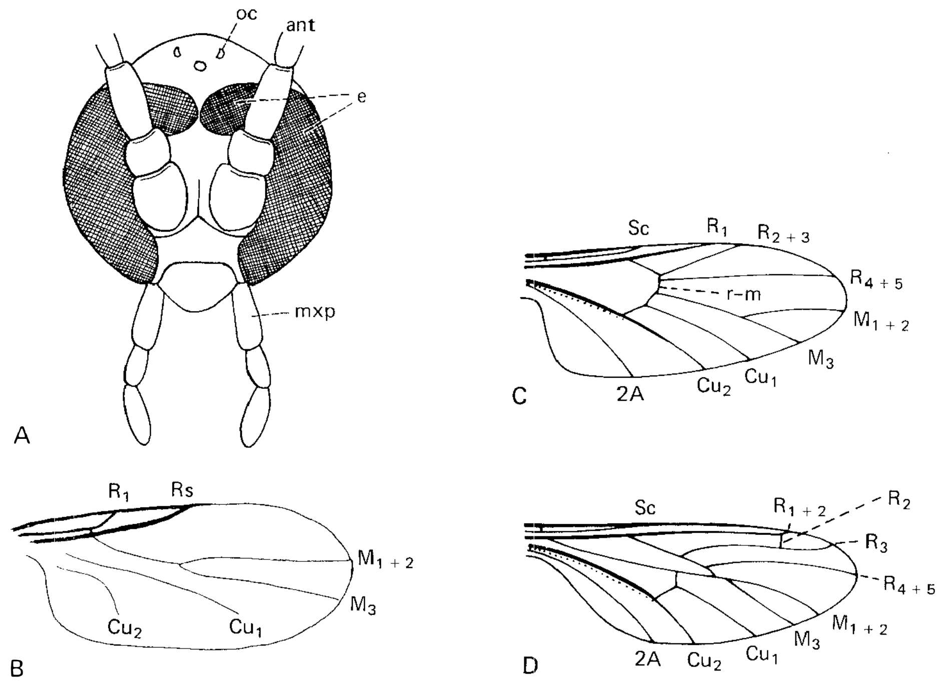

Figure 34–9 A, head of *Sciara* (Sciaridae), anterodorsal view; B, wing of a scatopsid; C, wing of *Mycetobia* (Anisopodidae); D, wing of *Axymyia* (Axymyiidae). *ant*, antenna; *e*, compound eye; *mxp*, maxillary palp; *oc*, ocellus.

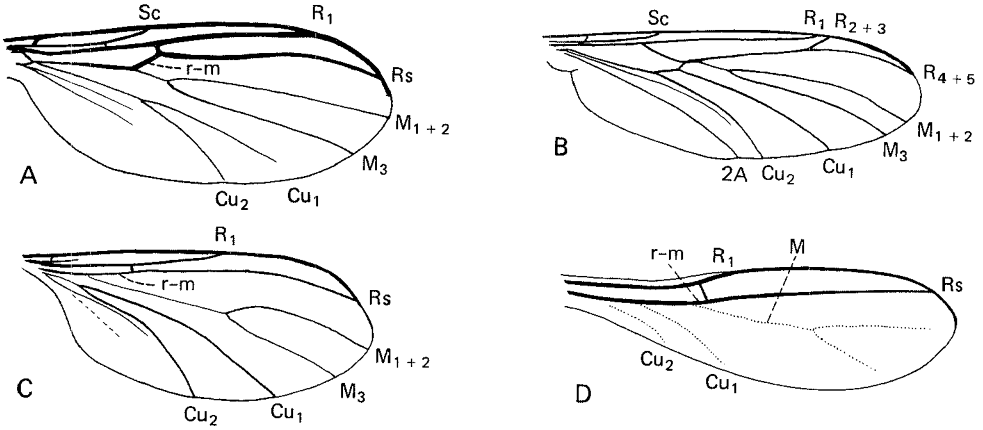

Figure 34–10 Wings of Mycetophilidae (A, B) and Sciaridae (C, D). A, Sciophilinae; B, Keroplatinae; C, *Sciara*; D, *Pnyxia*, male.

19′. Tibial spurs absent; Rs 3-branched, with R_2 appearing much like a crossvein and extending from R_{2+3} to about end of R_1 (Figure 34–9D) Axymyiidae* p. 715

20(19). Antennae usually shorter than thorax, rather stout, arising low on face, below compound eyes; second basal cell (M) present (Figure 34–8C); anal angle of wing usually well developed Bibionidae p. 715

20′.	Antennae variable, but usually longer than thorax, arising about middle of compound eyes or higher; second basal cell and wing shape variable	21	
21(20′).	Basal cells confluent, closed distally by r-m and m-cu; Rs forked opposite r-m; Sc complete, ending in C; 2A reaching wing margin (Figure 34–9C)	Anisopodidae (*Mycetobia*)*	p. 715
21′.	Basal cells variable; Rs simple or forked, if forked the fork is distad of r-m, or r-m is obliterated by the fusion of Rs and M; Sc and 2A variable; a large and widespread group	Mycetophilidae[2]	p. 718
22(9′).	C ending at or near wing tip (Figure 34–8A–F)	23	
22′.	C continuing around wing tip, though often weaker behind (Figure 34–8G–I)	25	
23(22).	Wings broad, posterior veins weak (Figure 34–8D); antennae about as long as head; dark-colored flies, rarely over 3 mm long, with a somewhat humpbacked appearance	Simuliidae	p. 714
23′.	Wings narrower and posterior veins stronger (Figure 34–8E,F); antennae much longer than head; habitus usually not as in the preceding entry	24	
24(23′).	M usually 2-branched (Figure 34–8E), M_3 rarely weak or absent; head rounded behind; metanotum rounded, without median furrow or keel; legs of moderate length, hind pair the longest; pulvilli absent; anterior thoracic spiracle nearly round; female mouthparts usually with mandibles and fitted for piercing	Ceratopogonidae	p. 708
24′.	M unbranched (Figure 34–8F); head flattened behind; metanotum generally with median furrow or keel; legs long, front legs usually the longest; pulvilli present or absent; anterior thoracic spiracle distinctly oval; mouthparts without mandibles, not fitted for piercing	Chironomidae	p. 709
25(22′).	First tarsal segment much shorter than second, tarsi sometimes appearing 4-segmented; small, fragile midges with weakly veined wings, the wings usually with fewer than 7 longitudinal veins (Figure 34–8A)	Cecidomyiidae	p. 716
25′.	First tarsal segment longer than second, tarsi clearly 5-segmented; other characters variable	26	
26(25′).	Antennae short, about as long as head, 2 basal segments thick, globose; wings with 6–7 veins reaching wing margin	Thaumaleidae*	p. 714
26′.	Antennae at least twice as long as head, 2 basal segments not as in the preceding entry; wings with 9–11 veins reaching wing margin	27	
27(26′).	Wings broad, pointed apically, usually densely hairy, and often held rooflike over body at rest; Rs usually 4-branched, M 3-branched (Figure 34–8G)	Psychodidae	p. 708
27′.	Wings usually long and narrow, or if broad not pointed apically, and not densely hairy although scales may lie along the wing veins or wing margin; Rs with 3 or fewer branches, M 2-branched (Figure 34-8H,I)	28	
28(27′).	Proboscis long, extending far beyond clypeus (Figure 34–36); scales present on wing veins and wing margin, usually also on body	Culicidae	p. 710
28′.	Proboscis short, barely extending beyond clypeus; no scales on wing veins or body	29	
29(28′).	R_{2+3} somewhat arched at base (Figure 34–8H); wing veins with short, inconspicuous hairs; antennae with short sparse hairs	Dixidae	p. 714

[2] *Hesperodes johnsoni* Coquillett (Keroplatinae), reported from Massachusetts and New Jersey, lacks ocelli. It is 12 mm long, is a member of the subfamily Keroplatinae, and has a wing venation similar to that shown in Figure 34–10B.

29′.	R_{2+3} nearly straight at base; wing veins with long, dense, conspicuous hairs; antennae with abundant, long hairs in distinct whorls	30	
30(29′).	Clypeus with numerous setae; R_1 meeting costal margin near wing apex, closer to R_2 than to Sc	Chaoboridae	p. 709
30′.	Clypeus with very few setae; R_1 meeting costal margin near to apex of Sc than to R_2	Corethrellidae	p. 709
31(3′).	Empodia pulvilliform, tarsi with 3 pads (Figure 34–2B)	32	
31′.	Empodia bristlelike or absent, tarsi with not more than 2 pads (Figure 34–2A)	44	
32(31).	Head unusually small, rarely more than half as wide as thorax, placed low down, consisting almost entirely of eyes (both males and females are holoptic); body appearing humpbacked (Figure 34–50); calypteres very large	Acroceridae	p. 721
32′.	Head more than half as wide as thorax; eyes never holoptic in female; calypteres usually small	33	
33(32′).	Venation peculiar, branches of Rs and M more or less converging to apex of wing, M_{1+2} ending before wing tip (Figure 34–11I); wings with a composite vein extending from base of Rs to wing margin, ending as M_3+Cu_1; tibiae without apical spurs	Nemestrinidae*	p. 722
33′.	Venation normal, branches of Rs and M diverging to wing margin, branches of M ending well behind wing tip (Figures 34–4, 34–11A,B, 34–12); middle and hind tibiae usually with apical spurs	34	
34(33′).	C ending before wing tip; branches of R more or less crowded together near costal margin (Figure 34–11A); R_5 (or R_{4+5} when it is not forked) ending before wing tip; discal cell (*D*, Figure 34–11A) short, usually little longer than wide; tibial spurs usually absent	Stratiomyidae	p. 719
34′.	Without the preceding combination of characters	35	
35(34′).	Third antennal segment annulated (Figure 34–1C,D,F), or the antennae appearing to consist of more than 3 segments	36	
35′.	Third antennal segment more or less globular or oval, not annulated, usually bearing an elongate style	42	
36(35).	Postscutellum well developed (as in Figure 34–17B); calypteres large and conspicuous; R_4 and R_5 divergent, enclosing the wing tip (Figure 34–4A,B)	37	
36′.	Postscutellum not developed or only very weakly developed; calypteres small or vestigial; R_4 and R_5 variable	38	
37(36).	Both upper and lower calypteres large; first abdominal tergite with notch in middle of posterior margin and with median suture; anal cell closed (Figure 34–4A,B); antennae usually arising below middle of head	Tabanidae	p. 720
37′.	Upper calypter large, but lower calypter scarcely developed; first abdominal tergite without median notch or suture; anal cell open; antennae arising above middle of head	Pelecorhynchidae*	p. 720
38(36′).	Third antennal segment elongate, parallel-sided or tapering, with several annulations, and without distinct style	39	
38′.	Third antennal segment globular or oval, with terminal style or appearing to be 2- or 3-segmented	40*	
39(38).	M_3 cell open (Figure 34–12A,B); front tibiae with apical spur	Xylophagidae	p. 719
39′.	M_3 cell closed (Figure 34–12C); front tibiae without apical spurs	Xylomyidae	p. 719
40(38′).	Antennae appearing 5-segmented, third segment with short, thick, 2-segmented terminal style; front tibiae with apical spur; length 2–3 mm	Rhagionidae (*Bolbomyia*)*	p. 720

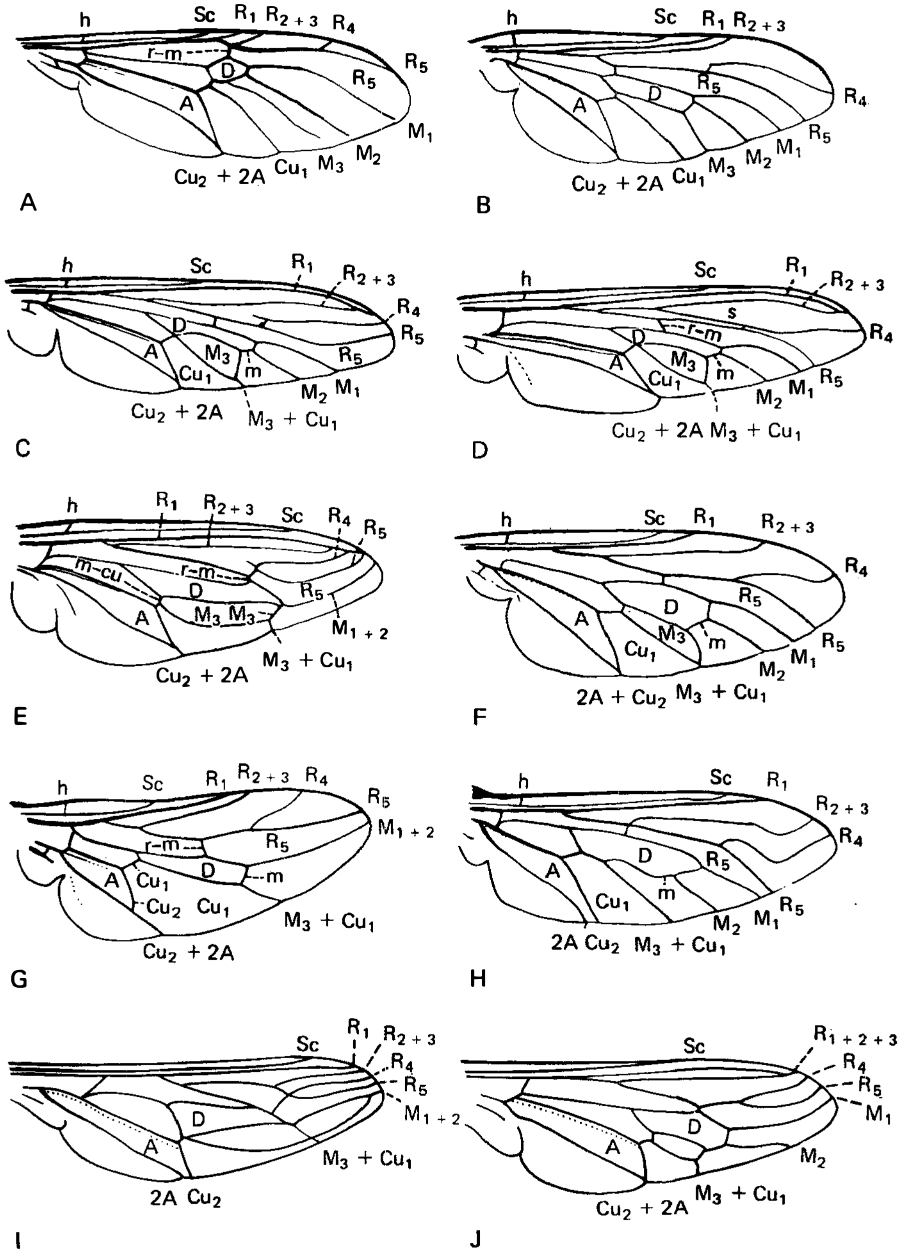

Figure 34–11 Wings of Brachycera. A, Stratiomyidae; B, Rhagionidae; C, Asilidae (*Efferia*); D, Asilidae (*Promachus*); E, Mydidae (*Mydas*); F, Therevidae; G, Scenopinidae; H, Bombyliidae; I, Nemestrinidae (*Neorhynchocephalus*); J, Apioceridae (*Apiocera*). *A*, anal cell; *D*, discal (first M_2) cell.

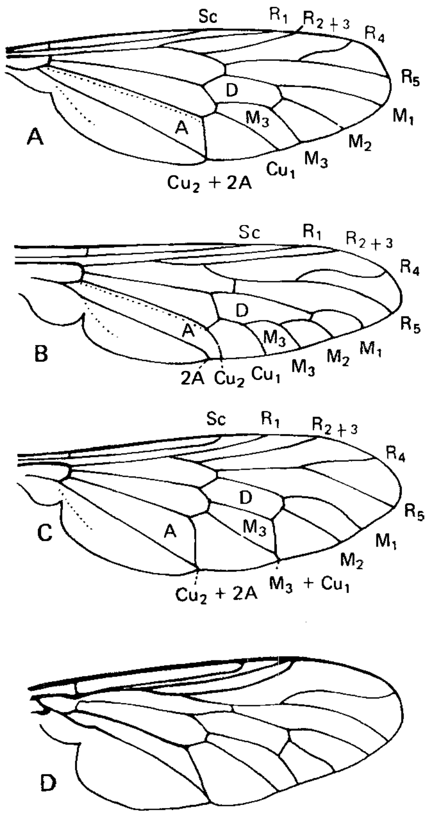

Figure 34–12 Wings of Brachycera. A, *Xylophagus* (Xylophagidae); B, *Coenomyia* (Xylophagidae); C, *Xylomya* (Xylomyidae); D, *Atherix* (Athericidae).

40′.	Antennae not as in the preceding entry, style on third antennal segment long and slender, and may or may not appear annulated; front tibiae with or without apical spurs	41*	
41(40′).	Front tibiae with 1–2 apical spurs	Xylophagidae (*Dialysis*)*	p. 719
41′.	Front tibiae without apical spurs	Rhagionidae*	p. 720
42(35′).	R$_1$ cell closed, R$_{2+3}$ meeting R$_1$ at wing margin (Figure 34–12D)	Athericidae*	p. 719
42′.	R$_1$ cell open, R$_{2+3}$ meeting C well beyond end of R$_1$	43	
43(42′).	Wings narrowed basally, without alula; scutellum bare; slender flies, about 5 mm long; western United States	Vermileonidae*	p. 721
43′.	Wings not so narrow basally, an alula nearly always present; scutellum hairy; size variable, but mostly over 5 mm long; widely distributed	Rhagionidae	p. 720
44(31′).	Coxae widely separated (Figure 34–13A); body somewhat flattened; ectoparasites of birds or mammals	Hippoboscidae	p. 731
44′.	Coxae close together (ventral view); body usually not particularly flattened; not ectoparasitic	45	
45(44′).	Wings with branches of R strongly thickened and crowded into anterior base of wing, behind R, 3–4 weak veins with no crossveins beyond base of wing (Figure 34–14G); hind legs long, femora flattened laterally; small, humpbacked flies, 1–4 mm long (Figure 34–59)	Phoridae	p. 727

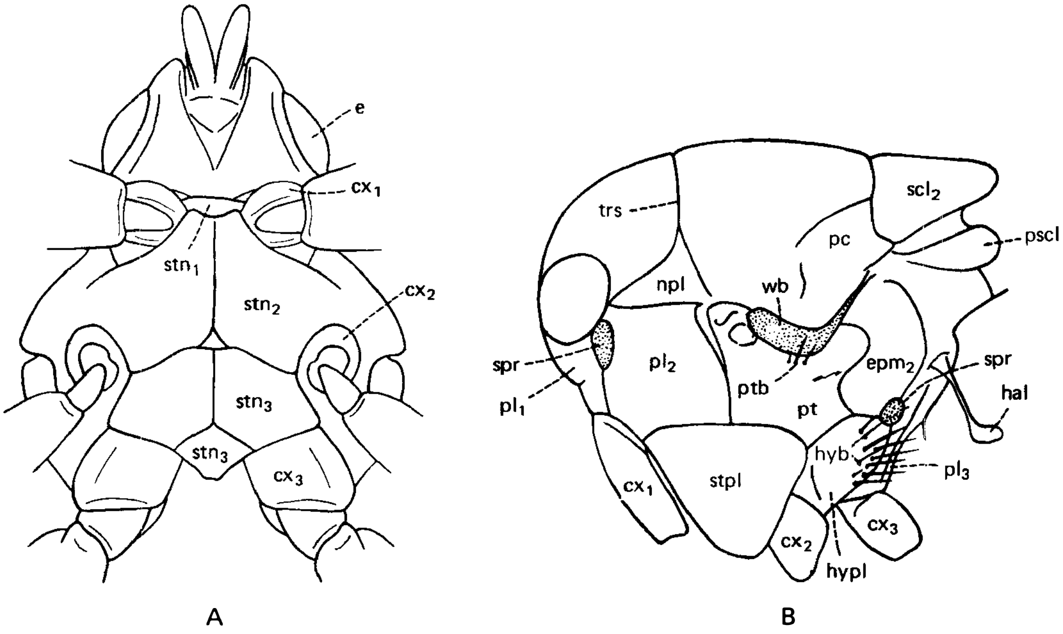

Figure 34–13 Thorax structure in muscoids. A, thorax of a hippoboscid (*Lynchia*), ventral view; B, thorax of a tachinid (*Ptilodexia*), lateral view. *cx*, coxa; *e*, compound eye; epm_2, mesepimeron; *hal*, haltere; *hc*, humeral callus; *hyb*, hypopleural bristles; *hypl*, hypopleuron; *npl*, notopleuron; *pc*, postalar callus; pl_1, propleuron; pl_2, mesopleuron; pl_3, metapleuron; *pscl*, postscutellum; *pt*, pteropleuron; *ptb*, pteropleural bristles; scl_2, mesoscutellum; *spr*, spiracle; stn_1, prosternum; stn_2, mesosternum; stn_3, metasternum; *stpl*, sternopleuron; *trs*, transverse suture; *wb*, base of wing. Only the hypopleural and pteropleural bristles are shown in B.

45′.	Without the preceding combination of characters	46	
46(45′).	Wings pointed at apex, with no crossveins except at base (Figure 34–14H); third antennal segment rounded, with terminal arista; small, slender, brownish or yellowish flies, 2–5 mm long	Lonchopteridae	p. 727
46′.	Wings rounded at apex, almost always with crossveins beyond base of wing; antennae, size, shape, and color variable	47	
47(46′).	Rs 3-branched	48	
47′.	Rs 2-branched or unbranched	55	
48(47).	The branches of Rs and M_1 (or M_{1+2}) ending before wing tip (Figure 34–11E); large, asilidlike flies	49	
48′.	M_1 (or M_{1+2}) ending behind wing tip; size and form variable	50	
49(48).	With 1 ocellus or none; antennae long, appearing 4-segmented, clubbed (Figure 34–54); widely distributed	Mydidae	p. 724
49′.	With 3 ocelli; antennae shorter, about as long as head, appearing 3-segmented, third segment tapering, not clubbed; occurring in arid regions of the West	Apioceridae*	p. 722
50(48′).	Vertex sunken, top of head concave between compound eyes (Figure 34–51D), eyes never holoptic	Asilidae	p. 723

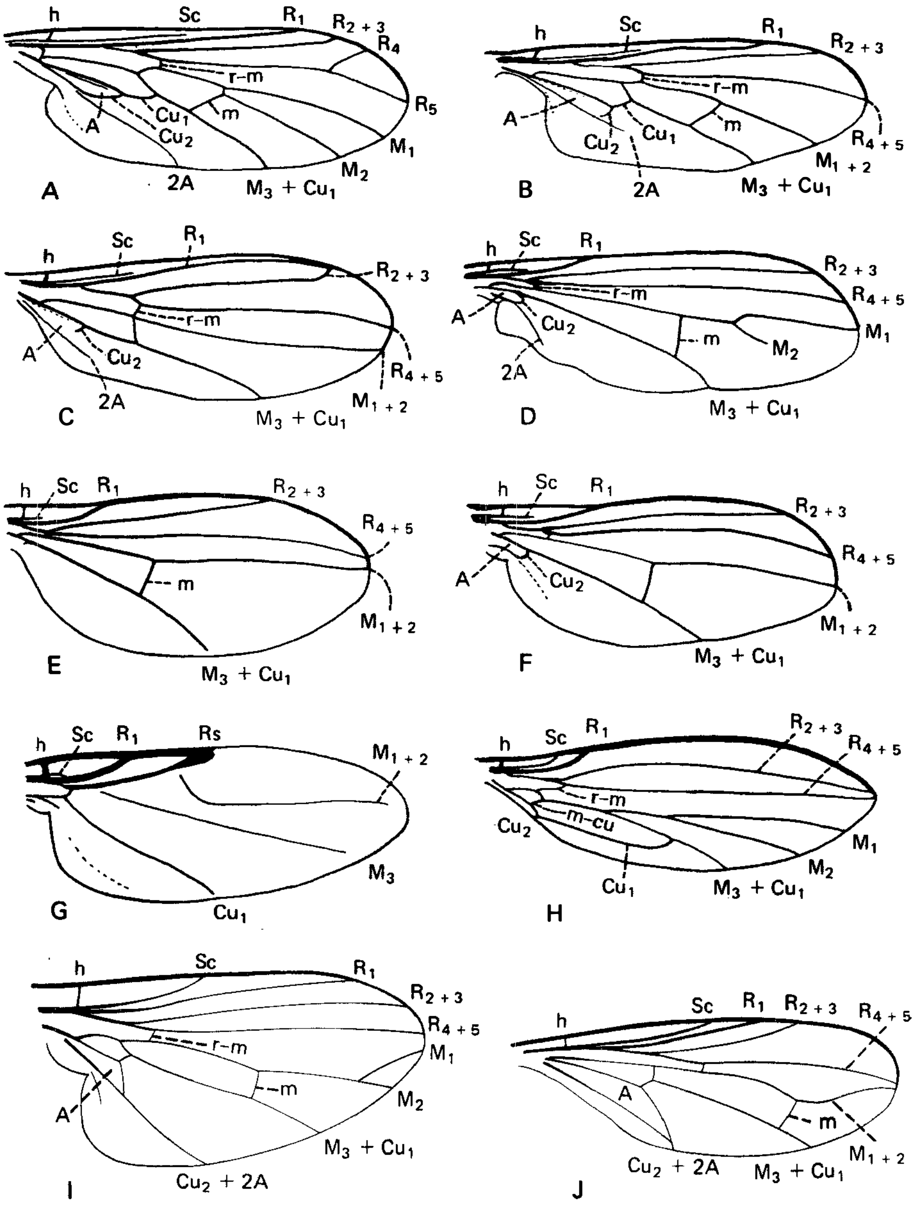

Figure 34–14 Wings of Brachycera. A–C, Empididae; D–F, Dolichopodidae; G, Phoridae; H, Lonchopteridae, female; I, Platypezidae; J, Pipunculidae. *A*, anal (1A) cell.

50′.	Vertex not sunken, the eyes often holoptic in males	51	
51(50′).	With 5 posterior cells, m-cu present, M_3 and Cu_1 separate or fused at base only (Figure 34–11F)	Therevidae	p. 725
51′.	With 4 or fewer posterior cells, if with 5 (some *Caenotus*, family Bombyliidae, Figure 34–56C) then bases of M_3 and Cu_1 fused and m-cu absent	52	
52(51′).	M_{1+2} ending at or in front of wing tip (Figure 34–11G) or fused distally with R_{4+5}; 3 posterior cells	Scenopinidae	p. 725

52′.	M_1 (or M_{1+2}) ending behind wing tip; 3 or 4 posterior cells (Figures 34–11H, 34–14A)	53	
53(52′).	Anal cell open (Figure 34–9H), or closed near wing margin and apex acute; body often hairy and robust	54	
53′.	Anal cell closed far from wing margin (Figure 34–14A) or absent, or if closed near wing margin apex is not acute; body rarely hairy, usually not robust	Empididae	p. 725
54(53).	Discal cell present; or if absent then R_{4+5} and M_{1+2} are not similarly forked, wings hyaline or patterned; usually over 5 mm long	Bombyliidae	p. 724
54′.	Discal cell absent; R_{4+5} and M_{1+2} similarly forked, each fork shorter than its stem; wings hyaline to pale brown; small flies, usually less than 5 mm long	Hilarimorphidae*	p. 724
55(47′).	Second antennal segment longer than third, third segment with a dorsal arista	Sciomyzidae (*Sepedon*)	p. 739
55′.	Second antennal segment not or scarcely longer than third, arista variable	56	
56(55′).	Hind tarsi, at least in male, nearly always with 1 or more segments expanded or flattened; wings relatively broad basally; anal angle well developed; anal cell closed some distance from wing margin, pointed apically (Figure 34–14I); M_{1+2} often forked apically; no frontal suture; arista terminal; small, usually black flies, less than 10 mm long	Platypezidae*	p. 728
56′.	Without the preceding combination of characters	57	
57(56′).	Anal cell elongate, longer than second basal cell, usually pointed apically, and narrowed or closed near wing margin (Figures 34–14J, 34–15); no frontal suture; head bristles usually lacking	58	
57′.	Anal cell usually shorter, closed some distance from wing margin, or lacking; if anal cell is elongate and pointed apically (Figure 34–22C), then a frontal suture is present and head bristles are usually present	62	
58(57).	Proboscis usually very long and slender, often twice as long as head or longer, often folding; face broad, with grooves below antennae; abdomen clavate, bent downward at apex (Figure 34–73); R_5 cell closed, pointed apically (Figure 34–15D)	Conopidae	p. 735

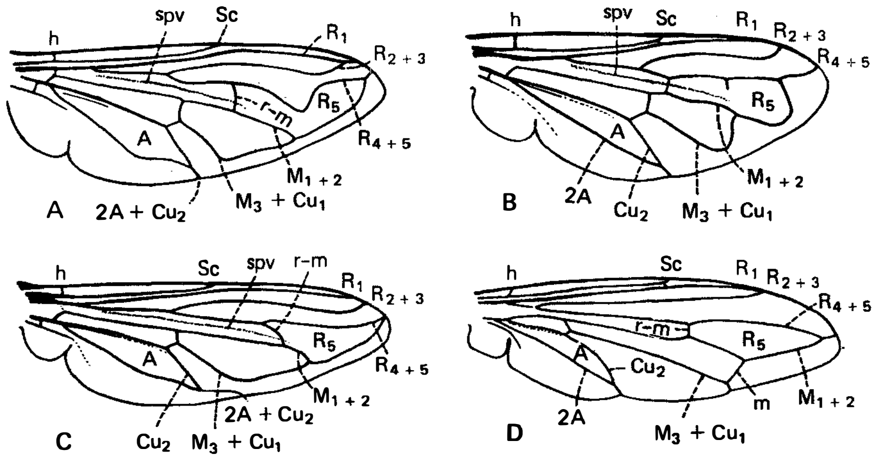

Figure 34–15 Wings of Syrphidae (A–C) and Conopidae (D). A, *Eristalis*; B, *Microdon*; C, *Spilomyia*; D, *Physocephala*. *A*, anal (1A) cell; *spv*, spurious vein.

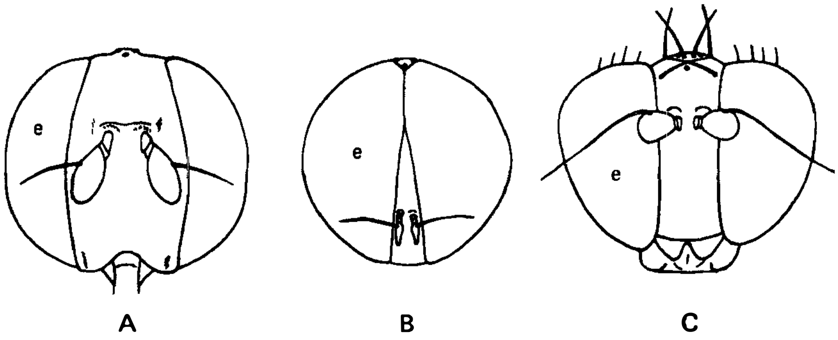

Figure 34–16 Heads of Diptera, anterior view. A, Syrphidae (*Metasyrphus*); B, Pipunculidae (*Pipunculus*); C, Dolichopodidae (*Dolichopus*). *e*, compound eye.

58′.	Proboscis short; face narrow, without grooves below antennae; abdomen and R_5 cell variable	59	
59(58′).	R_5 cell closed; usually a spurious vein crossing r-m between R_{4+5} and M_{1+2} (Figure 34–15A–C)	Syrphidae	p. 728
59′.	R_5 cell open, though sometimes narrowed apically; no spurious vein	60	
60(59′).	Head very large, hemispherical, face very narrow (Figures 34–16B, 34–60); proboscis small and soft	Pipunculidae	p. 727
60′.	Head not unusually large, face normal; proboscis slender and rigid	61	
61(60′).	R_{2+3} usually very short and ending in R_1, rarely lacking or ending in C beyond end of R_1; minute flies, 1.2–4.0 mm long, rather stocky in build, with a humpbacked appearance, usually brownish or grayish; mostly western United States	Bombyliidae (Cyrtosiinae and Mythicomyiinae)	p. 724
61′.	R_{2+3} ending in C well beyond end of R_1; relatively slender flies, usually black, size variable	Empididae (Hybotinae)	p. 725
62(57′).	Frontal suture absent (Figure 34–16)	63	
62′.	Frontal suture present (Figures 34–5A, 34–23, 34–27)	65	
63(62).	Head very large, hemispherical, face very narrow (Figures 34–16B, 34–60)	Pipunculidae (*Chalarus*)	p. 727
63′.	Head not unusually large; face variable	64	
64(63′).	The r-m crossvein located in basal fourth of wing, or absent; fork of Rs usually swollen (Figure 34–14D–F); male genitalia often folded forward under abdomen (Figure 34–58); body usually metallic	Dolichopodidae	p. 726
64′.	The r-m crossvein located beyond basal fourth of wing, fork of Rs usually not swollen (Figure 34–14B,C); male genitalia terminal, not folded forward under abdomen (Figure 34–57); body not metallic	Empididae	p. 725
65(62′).	Mouth opening small, mouthparts vestigial (Figure 34–17A); body hairy but not bristly, insect beelike in appearance, 9–25 mm long; R_5, sometimes also M_{1+2}, ending before wing tip (Figure 34–18E,F); bot and warble flies	Oestridae*	p. 732
65′.	Mouth opening normal, mouthparts present, functional; body usually with bristles; size, R_5, M_{1+2} variable	66	
66(65′).	Second antennal segment with a longitudinal suture on outer side (Figure 34–19A); thorax usually with a complete transverse suture (Figure 34–19C); lower (innermost) calypter usually large (calyptrate muscoid flies, except *Loxocera*, family Psilidae)	67	
66′.	Second antennal segment without such a suture (Figure 34–19B); thorax usually without complete transverse suture (Figure 34–19D); lower calypter usually small or rudimentary (acalyptrate muscoid flies)	76	
67(66).	Hypopleura and pteropleura with row of bristles (Figure 34–13B); R_5 cell narrowed or closed distally	68	

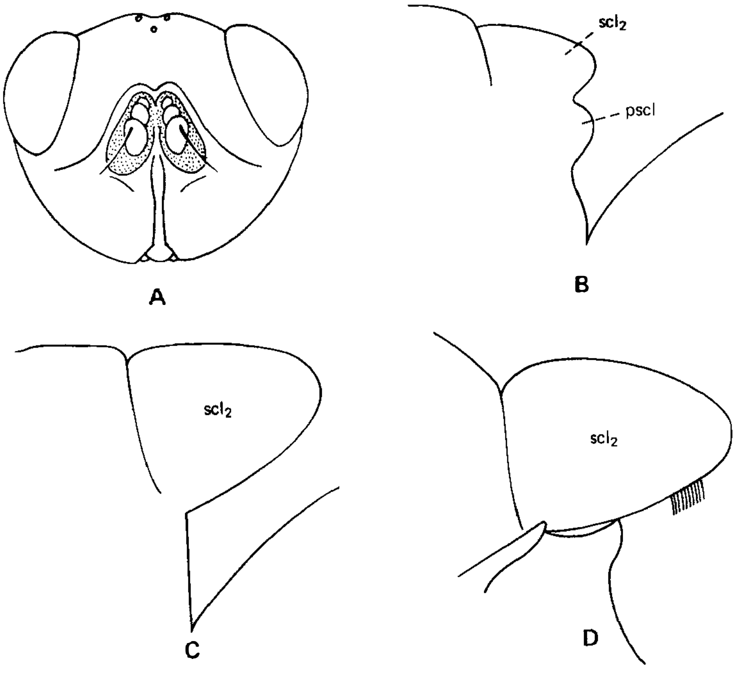

Figure 34–17 Characters of muscoid flies. A, head of a horse bot fly (*Gasterophilus*, Oestridae), anterior view; B–D, posterior part of the thorax, lateral view: B, *Hypoderma* (Oestridae); C, a robust bot fly (*Cuterebra*, Oestridae); D, an anthomyiid. *pscl*, postscutellum; *scl_2*, mesoscutellum.

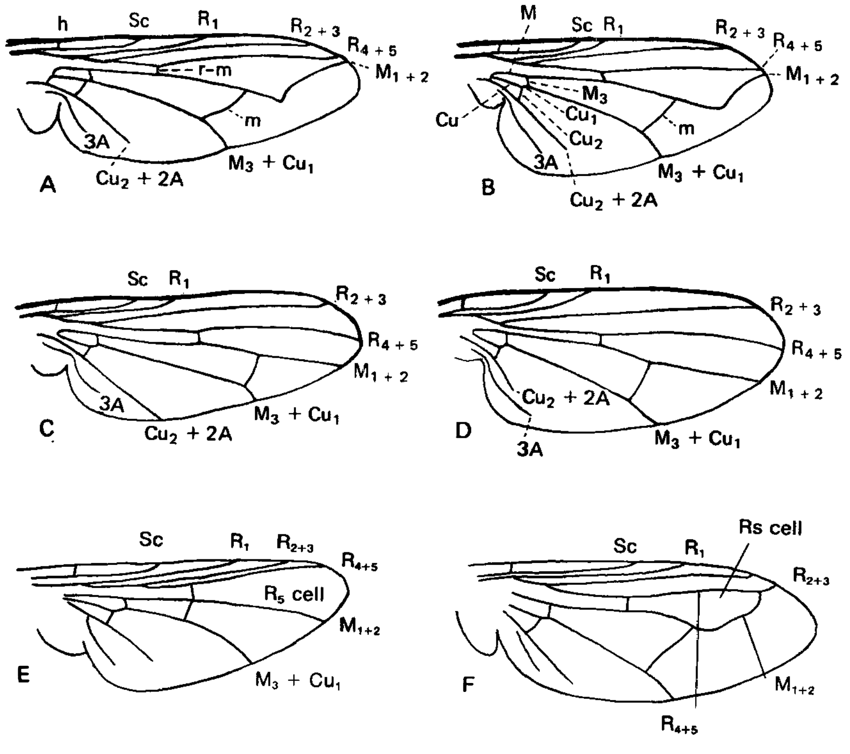

Figure 34–18 Wings of calyptrate muscoid flies. A, Tachinidae; B, Muscidae (*Musca*); C, Scathophagidae; D, Fanniidae (*Fannia*); E, *Gasterophilus* (Oestridae); F, *Oestrus* (Oestridae).

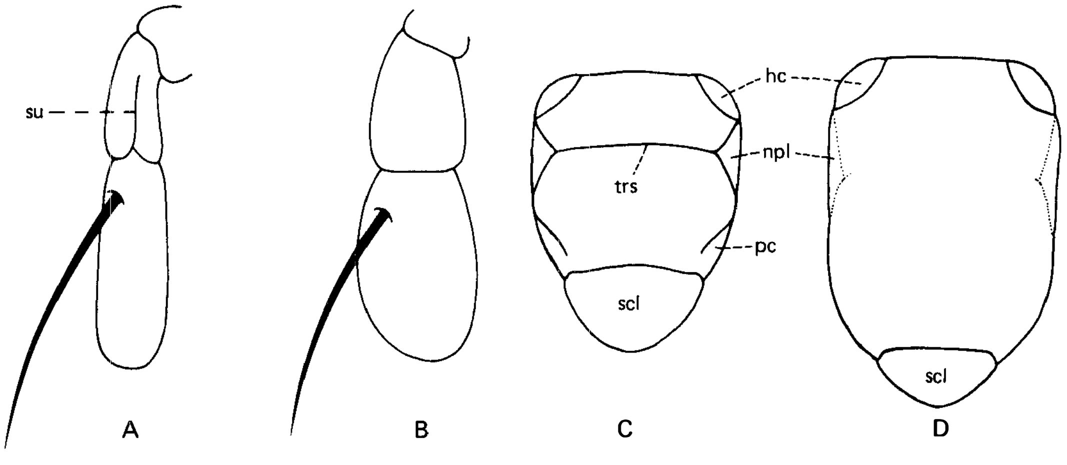

Figure 34–19 Antennae (A, B) and mesonota (C, D) of muscoid flies. A, calyptrate, showing suture (*su*) on second segment; B, acalyptrate, which lacks a suture on the second segment; C, calyptrate; D, acalyptrate. *hc*, humeral callus; *npl*, notopleuron; *pc*, postalar callus; *scl*, scutellum; *su*, suture; *trs*, transverse suture.

67′.	Hypopleura usually without bristles; if hypopleural bristles are present, then there are no pteropleural bristles, or proboscis is rigid and fitted for piercing, or R_5 cell is not narrowed distally	71	
68(67).	Postscutellum strongly developed (Figure 34–13B, *pscl*); arista usually bare	Tachinidae	p. 734
68′.	Postscutellum not developed or only weakly developed, if weakly developed (Rhinophoridae) upper half more or less membranous and concave in profile	69	
69(68′).	Postscutellum weakly developed; calypteres narrow, their inner margins bending away from scutellum; M_{1+2} bending forward apically and meeting R_{4+5}, R_5 cell closed	Rhinophoridae*	p. 733
69′.	Postcutellum not at all developed; calypteres not as in the preceding entry; M_{1+2} bending forward distally, but R_5 cell narrowly open at wing margin (as in Figure 34–18A)	70	
70(69′).	Usually 2 (rarely 3) notopleural bristles, hindmost posthumeral bristle located laterad of presutural bristle (Figure 34–20A); arista usually plumose beyond basal half; body often metallic, the thorax rarely or never with black stripes on a gray background	Calliphoridae	p. 729
70′.	Usually 4 notopleural bristles, and hindmost posthumeral bristle located even with or mesad of presutural bristle (Figure 34–20B); arista generally plumose only in basal half; body not metallic, the thorax often with black stripes on a gray background	Sarcophagidae	p. 733
71(67′).	Third antennal segment longer than arista (Figure 34–21); oral vibrissae absent; mesonotum without bristles except above wings	Psilidae (*Loxocera*)	p. 735
71′.	Third antennal segment not lengthened as in preceding entry; oral vibrissae present; mesonotum with bristles	72	
72(71′).	Sixth vein (Cu_2+2A) usually reaching wing margin, at least as a fold (Figure 34–18C), or if not (some Scathophagidae) then lower calypter linear and R_5 cell not narrowed apically	75	

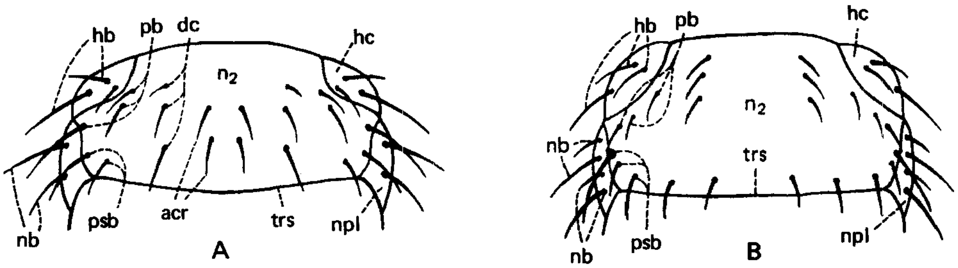

Figure 34–20 Anterior part of mesonotum of A, a blow fly (*Calliphora*), and B, a flesh fly (*Sarcophaga*). *acr*, acrostichal bristles; *dc*, dorsocentral bristles; *hb*, humeral bristles; *hc*, humeral callus; n_2, mesonotum; *nb*, notopleural bristles; *npl*, notopleuron; *pb*, posthumeral bristles; *psb*, presutural bristles; *trs*, transverse suture.

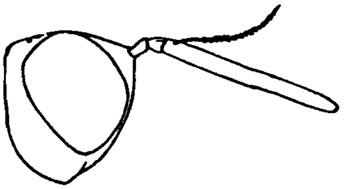

Figure 34–21 Head of *Loxocera* (Psilidae), lateral view.

72′.	Sixth vein never reaching wing margin, even as a fold (Figure 34–18B,D); R_5 cell variable, but often narrowed apically (Figure 34–18B)	73	
73(72′).	Dorsal surface of hind tibia with both preapical bristle and submedian bristle near its midlength; Cu_2+2A, if extended, meeting 3A before margin of wing (Figure 34–18D)	Fanniidae	p. 731
73′.	Dorsal surface of hind tibia with only preapical bristle, usually near apex but sometimes near two thirds length of tibia; Cu_2+2A, if extended, not meeting 3A	74	
74(73′).	Hind coxa with row of setae on posterior surface; Cu_2+2A short, ending less than halfway between its basal origin and wing margin	Fanniidae	p. 731
74′.	Hind coxa either without setae on posterior surface, or if present, then Cu_2+2A extending more than halfway to wing margin	Muscidae	p. 731
75(72).	Scutellum with fine, erect hairs on ventral surface (Figure 34–17D), or if such hairs absent (Fucelliinae) then cruciate frontal bristles present; usually 2–4 sternopleural bristles	Anthomyiidae	p. 729
75′.	Scutellum without fine hairs on ventral surface; cruciate frontal bristles absent; usually only 1 sternopleural bristle	Scathophagidae	p. 733
76(66′).	Proboscis very long and slender, often 2 or more times as long as head, elbowed; second antennal segment longer than first; abdomen often clavate (Figure 34–73); anal cell usually long and pointed, longer than second basal cell (except in *Dalmannia* and *Stylogaster*; in *Stylogaster* the ovipositor is slender and as long as rest of body)	Conopidae	p. 735

76′. Proboscis usually short and stout, rarely longer than head; second antennal segment usually shorter than first (if longer, then anal cell is shorter than second basal cell); anal cell usually very short, or absent 77

77(76′). Sc complete or nearly so, ending in C or just short of it, and free from R_1 distally (Figures 34–22, 34–23F); anal cell present 78

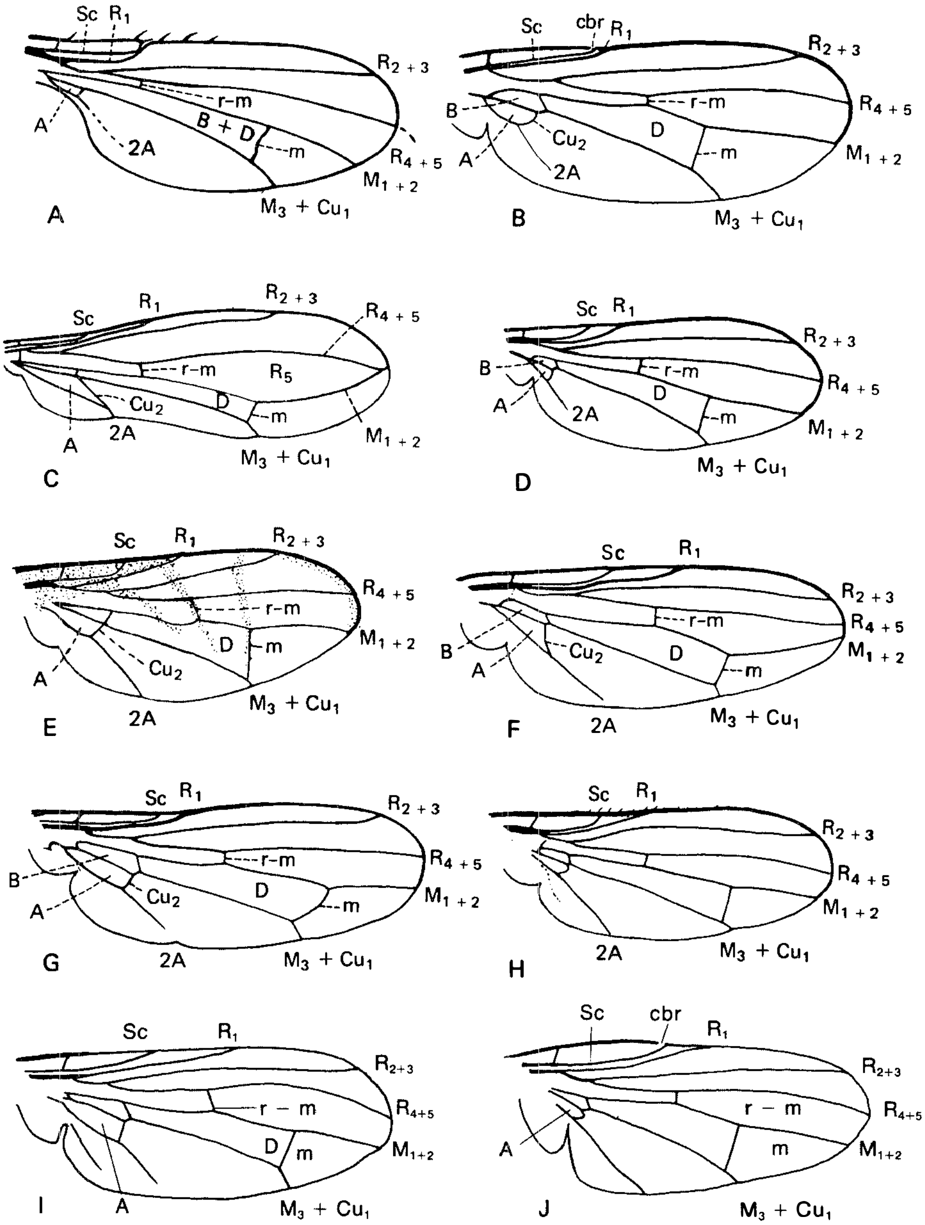

Figure 34–22 Wings of acalyptrate muscoid flies. A, Curtonotidae (*Curtonotum*); B, Piophilidae (*Piophila*); C, Micropezidae (*Taeniaptera*); D, Lauxaniidae (*Physegenua*); E, Platystomatidae (*Rivellia*); F, Ulidiidae (*Acrosticta*); G, Sciomyzidae (*Sepedon*); H, Heleomyzidae (*Amoebaleria*); I, Dryomyzidae (*Neurostena*); J, Lonchaeidae (*Lonchaea*). *A*, anal cell; *B*, second basal cell; *cbr*, costal break; *D*, discal (first M_2) cell.

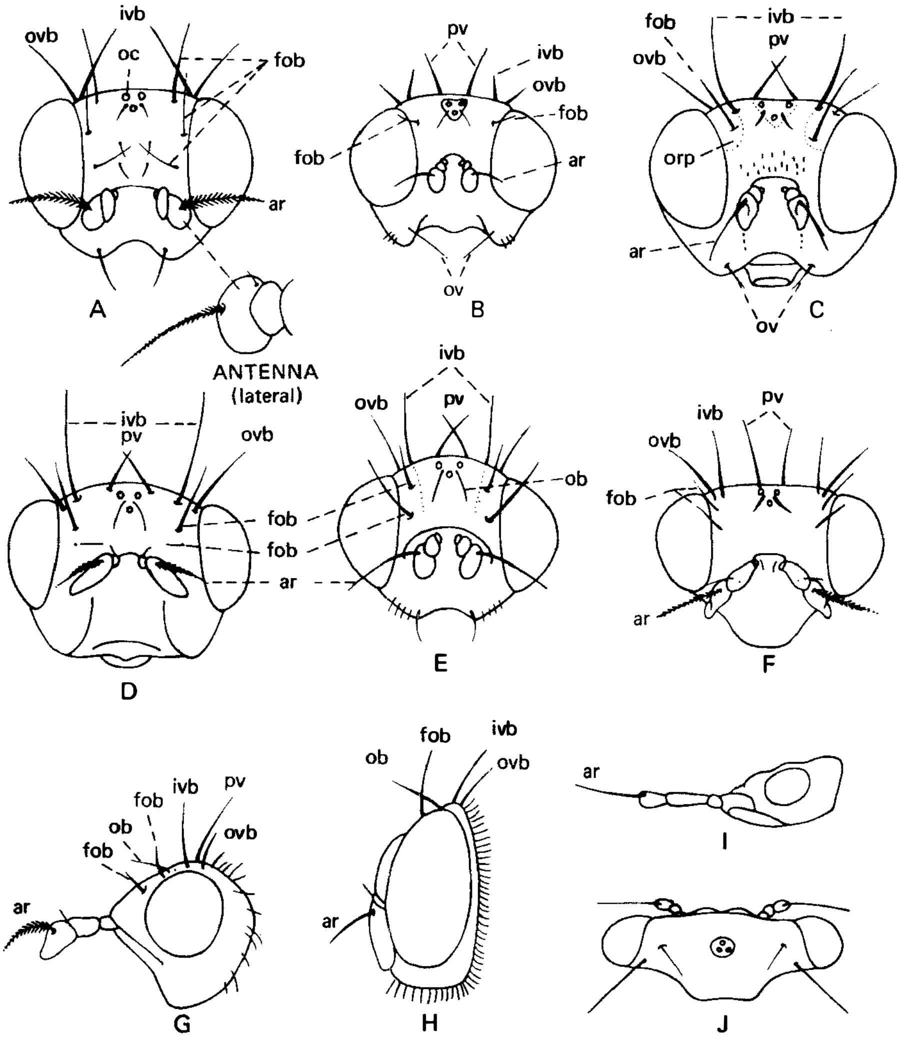

Figure 34–23 Heads of acalyptrate muscoid flies. A–F, anterior view; G–I, lateral view; J, dorsal view. A, Clusiidae (*Clusia*); B, Piophilidae (*Piophila*); C, Heleomyzidae (*Heleomyza*); D, Lauxaniidae (*Camptoprosopella*); E, Chamaemyiidae (*Chamaemyia*); F, G, Sciomyzidae (*Tetanocera*); H, Lonchaeidae (*Lonchaea*); I, Neriidae (*Odontoloxozus*); J, Diopsidae (*Sphyracephala*). *ar*, arista; *fob*, fronto-orbital bristles; *ivb*, inner vertical bristles; *ob*, ocellar bristles; *oc*, ocellus; *orp*, orbital plate; *ov*, oral vibrissae; *ovb*, outer vertical bristles; *pv*, postvertical bristles.

77′.	Sc incomplete, not reaching C, often fusing with R_1 distally (Figure 34–24A,B); anal cell present or absent	109	
78(77).	Ocelli present; size variable; wings with or without coloring	79	
78′.	Ocelli absent; medium-sized to large flies, often with considerable coloring in wings (Figure 34–75)	Pyrgotidae*	p. 736
79(78).	Head more or less produced laterally, with antennae widely separated (Figure 34–23J); scutellum bituberculate; front femora much swollen	Diopsidae*	p. 735

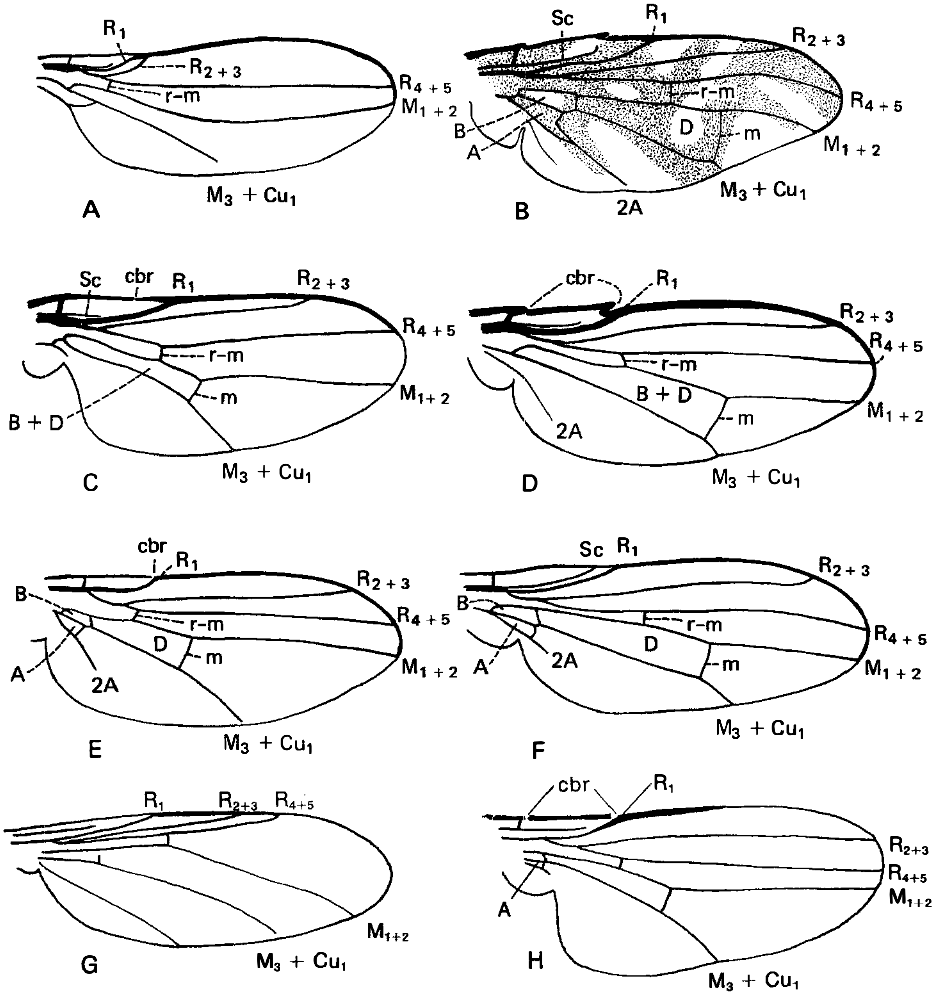

Figure 34–24 Wings of acalyptrate muscoid flies. A, Asteiidae (*Asteia*) (redrawn from Curran); B, Tephritidae; C, Chloropidae (*Epichlorops*); D, Ephydridae (*Ephydra*); E, Agromyzidae (*Agromyza*); F, Chamaemyiidae (*Chamaemyia*); G, Hippoboscidae (*Lynchia*); H, Milichiidae. *A*, anal cell; *B*, second basal cell; *cbr*, costal break; *D*, discal (first M_2) cell.

79′.	Head not so produced laterally, antennae close together; scutellum and front femora usually not as in preceding entry	80	
80(79′).	Posterior thoracic spiracle with 1 bristle or more (Figure 34–25D, *spbr*); head spherical; abdomen elongate, narrowed at base (Figure 34–82); palps nearly always vestigial (except in *Orygma*)	Sepsidae	p. 739
80′.	Posterior thoracic spiracle without bristles; head and abdomen usually not as in the preceding entry; palps usually well developed	81	
81(80′).	Dorsum of thorax flattened; legs and abdomen conspicuously bristly (Figure 34–80); seashore species	Coelopidae	p. 738

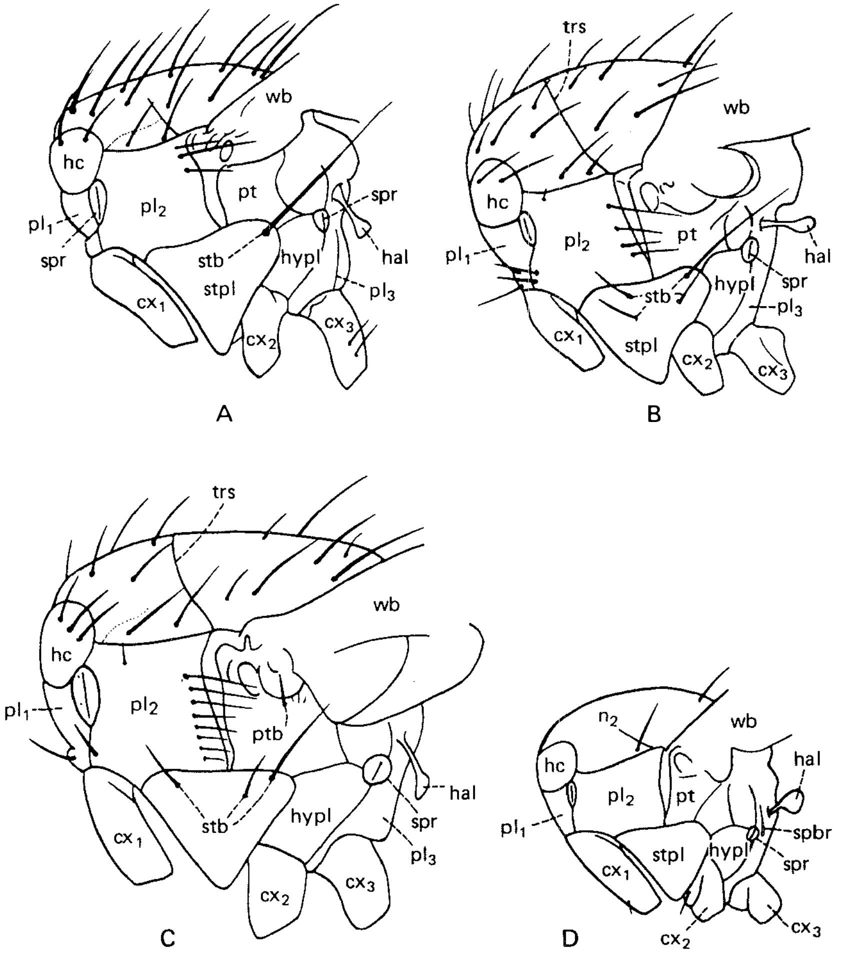

Figure 34–25 Thorax of muscoid flies, lateral view. A, Scathophagidae (*Scathophaga*); B, Anthomyiidae (*Anthomyia*); C, Muscidae (*Musca*); D, Sepsidae (*Themira*). *cx*, coxa; *hal*, haltere; *hc*, humeral callus; *hypl*, hypopleuron; n_2, mesonotum; pl_1, propleuron; pl_2, mesopleuron; pl_3, metapleuron; *pt*, pteropleuron; *ptb*, pteropleural bristles; *spbr*, spiracular bristle; *spr*, spiracle; *stb*, sternopleural bristles; *stpl*, sternopleuron; *trs*, transverse suture; *wb*, base of wing.

81′.	Dorsum of thorax convex, if rather flattened then legs are not bristly; widely distributed	82	
82(81′).	Eyes prominently bulging and vertex sunken; femora, especially hind femora, enlarged; medium-sized tropical flies, usually dark brown with yellowish markings and the wings not patterned; recorded from Florida, Arizona, and New Mexico	83*	
82′.	Eyes not prominently bulging and vertex not sunken; femora, size, color variable, but usually not as in preceding entry; widely distributed	84	
83(82).	A series of crossveins between C and R_{2+3}; R_1 ending close to Sc; R_5 cell not narrowed distally; Arizona and New Mexico	Ulidiidae*	p. 738
83′.	No crossveins between C and R_{2+3}; R_1 ending far beyond Sc; R_5 cell not narrowed distally; Florida	Ropalomeridae*	p. 739
84(82′).	Oral vibrissae present (Figure 34–23A,C, ov)	85	
84′.	Oral vibrissae absent (Figure 34–23F–I)	92	
85(84).	Costa spinose (Figure 34–22A,H)	86	

85′.	Costa not spinose	88	
86(85).	Second basal and discal cells confluent (Figure 34–22A, *B*+*D*); arista plumose	Curtonotidae*	p. 741
86′.	Second basal and discal cells separated (Figure 34–22B, *B* and *D*); arista usually not plumose	87	
87(86′).	Postverticals diverging; anal vein (2A) reaching wing margin; 4 or 5 sternopleurals; 2 pairs of fronto-orbitals; ocellar triangle large	Piophilidae (*Actenoptera*)*	p. 736
87′.	Postverticals converging; other characters usually not as in preceding entry	Heleomyzidae	p. 741
88(85′).	Second basal and discal cells confluent (as in Figure 34–22A, *B*+*D*); postverticals lacking	Aulacigastridae*	p. 740
88′.	Second basal and discal cells separated (Figure 34–22B, *B* and *D*); postverticals present	89	
89(88′).	Two to 4 pairs of fronto-orbitals; second antennal segment usually with angular projection on outer side (Figure 34–23A); arista subapical; color variable	Clusiidae	p. 740
89′.	At most 2 pairs of fronto-orbitals (Figure 34–23B); second antennal segment without angular projection on outer side; arista subbasal (Figure 34–23B); usually shining black or metallic bluish	90	
90(89′).	Postverticals diverging (Figure 34–23B); 2A not reaching wing margin (Figure 34–22B)	Piophilidae	p. 736
90′.	Postverticals converging; 2A variable	91*	
91(90′).	2A reaching wing margin; 1 pair of fronto-orbitals	Heleomyzidae (*Borboropsis* and *Oldenbergiella*, western Canada and Alaska)*	p. 741
91′.	2A not reaching wing margin; 2 pairs of fronto-orbitals; widely distributed	Chyromyidae*	p. 741
92(84′).	Sc apically bent forward at almost a 90-degree angle and usually ending before reaching C (Figure 34–24B); C broken near end of Sc; wings usually patterned (Figures 34–76A, 34–77)	Tephritidae	p. 737
92′.	Sc apically bent toward C at a less abrupt angle and usually reaching C (Figure 34–22F); C not broken near end of Sc; wings variable	93	
93(92′).	C broken only near humeral crossvein; postverticals widely separated and diverging	Acartophthalmidae*	p. 739
93′.	C entire, broken only near end of Sc, or broken both near humeral crossvein and end of Sc; postverticals variable	94	
94(93′).	R_5 cell closed or much narrowed apically (Figure 34–22C); slender flies, the legs usually long and slender	95	
94′.	R_5 cell open, usually not narrowed apically; body shape and legs variable, but usually not as in preceding entry	97	
95 (94,116).	Arista apical (Figure 34–23I), southwestern United States	Neriidae*	p. 735
95′.	Arista dorsal; widely distributed	96	
96(95′).	Head in profile higher than long, eyes large, distinctly higher than long; anal cell rounded apically; no sternopleural bristles	Tanypezidae*	p. 735
96′.	Head in profile as long as or longer than high, eyes smaller, not much higher than long; anal cell square or pointed apically; 1 sternopleural bristle or none	Micropezidae	p. 734
97(94′).	Some or all tibiae with 1 or more preapical dorsal bristles (Figure 34–26B); C entire (Figure 34–22D,G,I); body usually light-colored, at least in part	98	

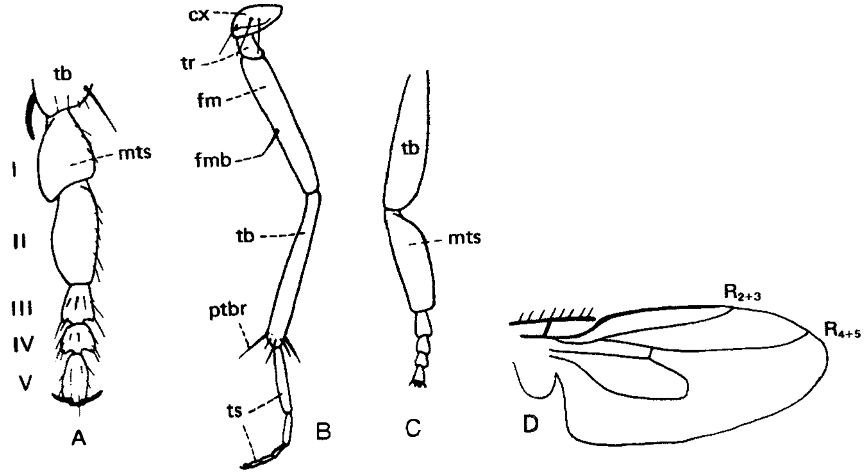

Figure 34–26 A, hind tarsus of *Copromyza* (Sphaeroceridae); B, middle leg of *Tetanocera* (Sciomyzidae); C, hind leg of *Agathomyia* (Platypezidae); D, wing of *Leptocera* (Sphaeroceridae). *cx*, coxa; *fm*, femur; *fmb*, femoral bristle; *mts*, first tarsal segment; *ptbr*, preapical tibial bristles; *tb*, tibia; *tr*, trochanter; *ts*, tarsus; *I–V*, tarsal segments 1–5.

97′.	Tibiae usually without preapical dorsal bristles; if such bristles are present then either ovipositor is long and sclerotized, or R_1 is setulose above, or the vein forming end of the anal cell is bent (Figure 34–22F); C entire or broken near end of Sc; color variable	100	
98(97).	Postverticals converging (Figure 34–23D); 2A short, not reaching wing margin (Figure 34–22D); small flies, rarely over 6 mm long	Lauxaniidae	p. 738
98′.	Postverticals parallel, diverging, or absent; 2A reaching wing margin, at least as a fold; size variable	99	
99(98′).	Femora with bristles, and a characteristic bristle usually present near middle of anterior face of middle femur (Figure 34–26B); R_1 ending at middle of wing (Figure 34–22G); antennae usually projecting forward and the face generally produced (Figure 34–23G)	Sciomyzidae*	p. 739
99′.	Femoral bristles not developed; R_1 ending beyond middle of wing (Figure 34–22I); antennae usually not projecting forward	Dryomyzidae*	p. 739
100(97′).	Cu_2 bent distad in middle, anal cell with acute distal projection posteriorly (Figures 34–22F and as in 34–24B); wings usually patterned	Ulidiidae	p. 738
100′.	Cu_2 straight or curved basad, anal cell without acute distal projection posteriorly (Figure 34–22E); wing color variable	101	
101(100′).	Costa broken near end of Sc	102	
101′.	Costa not broken near end of Sc (Figures 34–22E,F and 34–24F)	106	
102(101).	Second abdominal segment usually with lateral bristles; femora often thickened and spinose; wings usually patterned	Richardiidae*	p. 737
102′.	Second abdominal segment without lateral bristles; femora not thickened	103	
103(102′).	With 1 to several upcurved bristles below compound eye; 3–5 pairs of lateroclinate fronto-orbitals; postverticals diverging; seashore species	Canacidae*	p. 740
103′.	Without upcurved bristles below compound eye; fewer than 3 (usually 1) pair of lateroclinate fronto-orbitals; postverticals parallel or diverging; widely distributed	104	
104(103′).	Head hemispherical in profile, eyes large, oval or semicircular (Figure 34–23H); third antennal segment elongate (Figure 34–23H); postverticals diverging; 2A usually sinuate; small, shining, blackish flies with broad, flat abdomen; female with lancelike ovipositor	Lonchaeidae	p. 736

104′.	Head more or less rounded in profile, eyes smaller, rounded or slightly oval; postverticals parallel or slightly divergent; 2A not sinuate; pale-colored flies, or with yellow or reddish markings	105*	
105(104′).	Costa spinose (as in Figure 34–22A); eyes oval; Arizona and California (*Omomyia*)	Richardiidae*	p. 737
105′.	Costa not spinose; eyes round; southern United States and Canada	Pallopteridae*	p. 736
106(101′).	Postverticals converging (Figure 34–23E) or absent; R_1 bare above; small flies, usually gray	Chamaemyiidae	p. 738
106′.	Postverticals diverging or absent; R_1 bare or setulose above; small to medium-sized flies, usually dark and shining	107	
107(106′).	Eyes horizontally oval, about twice as long as high; length 1.5–2.5 mm; grayish flies with yellowish markings on sides of thorax and abdomen, and on front; recorded from New Mexico, Oregon, New Brunswick, and Newfoundland	Chamaemyiidae (*Cremifania*)*	p. 738
107′.	Without the preceding combination of characters	108	
108(107′).	Anal cell relatively long, its anterior side more than one fourth as long as posterior side of discal cell (Figure 34–22E); sternopleural bristles lacking; R_1 setulose above	Platystomatidae	p. 738
108′.	Anterior side of anal cell less than one fourth as long as posterior side of discal cell; sternopleural bristles usually present; R_1 bare or setulose above	Ulidiidae	p. 738
109(77′).	Sc apically bent forward at almost a 90-degree angle and ending before reaching C (Figure 34–24B); C broken near end of Sc; anal cell usually with acute distal projection posteriorly (Figure 34–24B); wings usually patterned (Figures 34–76A, 34–77)	Tephritidae	p. 737
109′.	Sc and anal cell not as in preceding entry; wing color variable	110	
110(109′).	Basal segment of hind tarsi short, swollen, shorter than second segment (Figure 34–26A)	Sphaeroceridae	p. 741
110′.	Basal segment of hind tarsi normal, not swollen, longer than second segment	111	
111(110′).	Third antennal segment large, reaching almost to lower edge of head; arista absent, but a short spine or tubercle at apex of third antennal segment; eyes large, vertically elongate; small, dark-colored flies, less than 2 mm long; California	Cryptochetidae*	p. 741
111′.	Third antennal segment not as in preceding entry, arista present	112	
112(111′).	R_{2+3} short, ending in C close to or with R_1 (Figure 34–24A); postverticals diverging	Asteiidae*	p. 740
112′.	R_{2+3} longer, ending in C well beyond R_1 and beyond middle of wing (Figure 34–24C–F); postverticals variable	113	
113(112′).	Costa entire, with neither a humeral nor a subcostal break (Figure 34–24F)	114	
113′.	Costa with at least a subcostal break, sometimes also with a humeral break (Figure 34–24D)	118	
114(113).	Ocellar bristles present, although sometimes weak; arista variable	115	
114′.	Ocellar bristles absent; arista pubescent)	Aulacigastridae (*Stenomicra*)*	p. 740
115(114).	Anal cell and 2A present, distinct	116	
115′.	Anal cell and 2A atrophied, incomplete, or absent	117*	
116(115).	R_5 cell narrowed apically; legs long, slender	95	

116′.	R_5 cell not narrowed apically; legs usually not long and slender	Chamaemyiidae	p. 738
117(115′).	R_1 joining C in basal third of wing; R_5 cell slightly narrowed distally; postverticals weak or absent; arista variable	Asteiidae (*Leiomyza*)*	p. 740
117′.	R_1 joining C near middle of wing; R_5 cell not narrowed distally; postverticals short, diverging; arista plumose	Periscelididae*	p. 740
118(113′).	Costa broken only near end of Sc or R_1 (Figure 34–24C,E)	119	
118′.	Costa broken near end of Sc or R_1, and also near humeral crossvein (Figure 34–24D)	130	
119(118).	Anal cell present (Figure 34–24E); ocellar triangle variable	120	
119′.	Anal cell absent (Figure 34–24C); ocellar triangle large (Figure 34–27A)	Chloropidae	p. 741
120(119).	Costa spinose (as in Figure 34–22A,H); oral vibrissae present; postverticals converging; orbital plates long, reaching nearly to level of antennae; usually with 2 pairs of fronto-orbitals that are reclinate or lateroclinate	Ulidiidae*	p. 738
120′.	Costa not spinose; other characters variable	121	
121(120′).	Oral vibrissae present	122	
121′.	Oral vibrissae absent	128	
122(121).	Ocellar triangle large (as in Figure 34–27A); 3–5 pairs of lateroclinate fronto-orbitals; postverticals diverging; flies living along the seashore	Canacidae*	p. 740

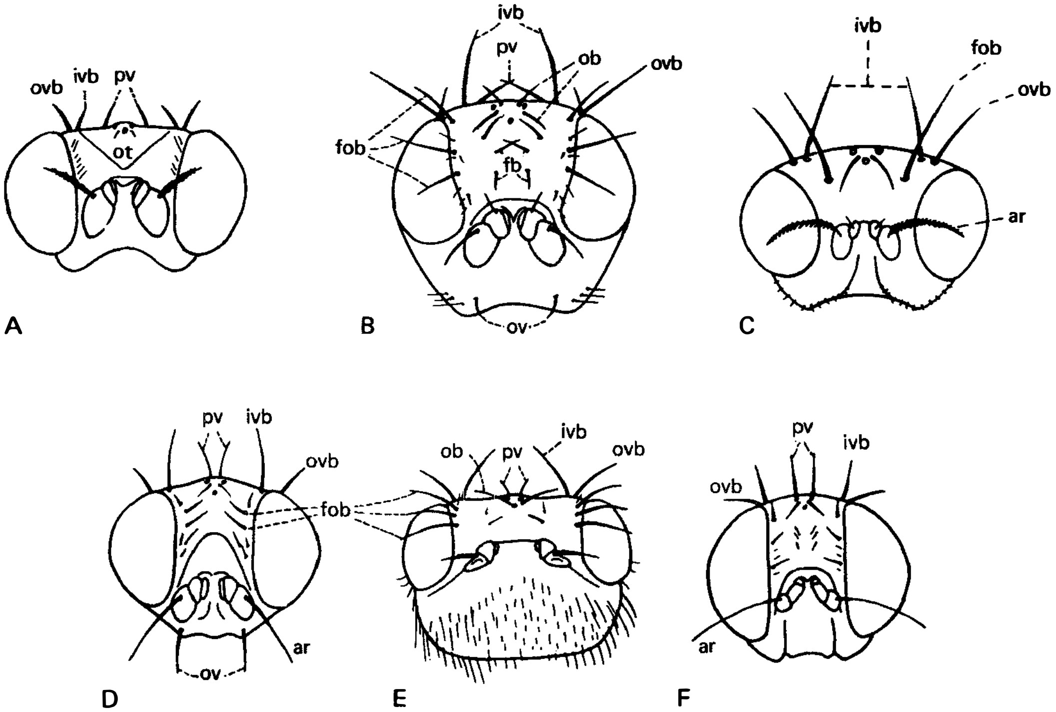

Figure 34–27 Heads of acalyptrate muscoid flies, anterior view. A, Chloropidae (*Diplotoxa*); B, Tethinidae (*Tethina*); C, Opomyzidae (*Opomyza*); D, Agromyzidae (*Agromyza*); E, Ephydridae (*Ephydra*); F, Milichiidae (*Milichia*). *ar*, arista; *fb*, frontal bristles; *fob*, fronto-orbital bristles; *ivb*, inner vertical bristles; *ob*, ocellar bristles; *ot*, ocellar triangle; *ov*, oral vibrissae; *ovb*, outer vertical bristles; *pv*, postvertical bristles.

122′.	Ocellar triangle small; other characters variable	123	
123(122′).	Wings strongly narrowed at base, anal angle not distinct	Opomyzidae (*Geomyza*)*	p. 740
123′.	Wings not so narrow at base, and with distinct anal angle	124	
124(123′).	Postverticals diverging	125	
124′.	Postverticals converging or absent	126	
125(124).	Wings patterned; preapical tibial bristles usually present; 2 reclinate and 1 inclinate pairs of fronto-orbitals	Odiniidae*	p. 740
125′.	Wings hyaline, not patterned; preapical tibial bristles absent; fronto-orbitals usually not as in preceding entry	Agromyzidae	p. 739
126(124′).	All fronto-orbitals directed outward (Figure 34–27B)	Tethinidae*	p. 741
126′.	Some or all fronto-orbitals reclinate, none directed outward	127	
127(126′).	Mesopleura bare	Anthomyzidae[3]	p. 740
127′.	Mesopleura setulose	Chyromyidae*	p. 741
128(121′).	Sternopleural bristles present; sometimes with spur in apical section of M_{1+2} extending into second posterior cell	Opomyzidae*	p. 740
128′.	Sternopleural bristle absent; M_{1+2} without a spur in apical section	129	
129(128′).	Mesopleura with large bristle in addition to fine hairs; usually 2 notopleural bristles	Tanypezidae*	p. 735
129′.	Mesopleura without large bristle, with fine hairs only; 1 notopleural bristle	Psilidae	p. 735
130(118′).	Anal cell present; postverticals usually well developed and converging; oral vibrissae usually present	131	
130′.	Anal cell absent; postverticals and oral vibrissae variable	139	
131(130).	Ocellar bristles present, well developed; frons never with a bright orange band; arista variable	132	
131′.	Ocellar bristles absent or very weak; frons with bright orange band near anterior margin; arista plumose	Aulacigastridae (*Aulacigaster*)*	p. 740
132(131).	Middle tibiae with preapical dorsal bristle; face tuberculate; arista bare or pubescent, not plumose	Heleomyzidae (*Cinderella*)*	p. 741
132′.	Middle tibiae usually without preapical dorsal bristle; face not tuberculate; arista variable, but often plumose	133	
133(132′).	All fronto-orbitals similarly oriented; arista with short pubescence; postverticals slightly converging; Arizona and Utah	Pseudopomyzidae*	p. 735
133′.	Fronto-orbitals not similarly directed; arista variable, but often plumose; postverticals variable; widely distributed	134	
134(133′).	At least 1 pair of fronto-orbitals bent inward (Figure 34–27F); oral vibrissae sometimes weak	135	
134′.	No fronto-orbitals bent inward; oral vibrissae well developed	136	
135(134).	Genae broad, with a row of bristles in middle; proboscis short and stout	Carnidae*	p. 741
135′.	Genae usually narrow, if broad then bristles confined to lower margin; proboscis variable, but often slender	Milichiidae	p. 741
136(134′).	Costa spinose (Figure 34–22A); arista with long plumose setae; proclinate fronto-orbital arising below reclinate fronto-orbital	Curtonotidae*	p. 741
136′.	Costa usually not spinose, or if spinose (Diastatidae) bristles short, extending beyond middle of wing; fronto-orbitals variable	137	
137(136′).	Costa spinose, bristles short, extending nearly to wing tip; proclinate fronto-orbital arising above reclinate fronto-orbital; arista with short plumose setae	Diastatidae*	p. 741

[3] The Pseudopomyzidae will key out here if one cannot see the costal break near the humeral crossvein.

137′.	Costa not spinose; proclinate fronto-orbital usually arising below reclinate fronto-orbital; arista with long plumose setae	138	
138(137′).	Sternopleural bristle present; body not metallic; anal cell well developed, closed apically; widely distributed, common flies	Drosophilidae	p. 741
138′.	Sternopleural bristle absent; body metallic; anal cell poorly developed, open apically; Ontario	Camillidae*	p. 741
139(130′).	Face strongly convex, usually without oral vibrissae (Figure 34–27E); postverticals, if present, diverging	Ephydridae	p. 742
139′.	Face somewhat concave; oral vibrissae and postverticals variable	140*	
140(139′).	Arista plumose; tibiae with preapical dorsal bristle; body metallic; Ontario	Camillidae*	p. 741
140′.	Arista slightly pubescent, not plumose; middle tibiae without preapical dorsal bristle; widely distributed	Carnidae*	p. 741
141(1′).	Antennal flagellum elongate, annulated basally, and clubbed; eyes separated dorsally but contiguous ventrally; small aquatic flies, less than 2 mm long, slender, pale, weakly sclerotized; found in rapid streams in Quebec, New Brunswick, and Appalachian Mountains south to Alabama	Nymphomyiidae*	p. 715
141′.	Without the preceding combination of characters	142*	
142(141′).	Antennae with 6 or more freely articulated segments; palps usually with 3–5 segments (Nematocera)	143*	
142′.	Antennae consisting of 3 or fewer segments; palps not segmented (Brachycera)	150*	
143(142).	Mesonotum with a V-shaped suture (as in Figure 34–28)	Tipulidae	p. 707
143′.	Mesonotum without a V-shaped suture	144*	
144(143′).	Compound eye consisting of a single facet; ocelli absent; head and thorax small, well sclerotized, abdomen thick, weakly sclerotized, indistinctly segmented; antennae thick, 8-segmented; length 3.4 mm; found in leaf litter in Virginia	Cecidomyiidae (*Baeonotus*)*	p. 716
144′.	Without the preceding combination of characters	145*	
145(144′).	At least 1 ocellus present	146*	
145′.	Ocelli absent	Chironomidae (*Clunio*, Florida; *Eretmoptera*, California)*	p. 709
146(145).	Tibiae with apical spurs	147*	
146′.	Tibiae without apical spurs	148*	
147(146).	Scutellum and halteres present; tarsal claws simple; wings present but only about half normal size; abdomen normal-sized	Scatopsidae (*Coboldia*)*	p. 718
147′.	Scutellum, halteres, and wings absent; tarsal claws variable; abdomen sometimes greatly swollen	Cecidomyiidae*	p. 716
148(146′).	Eyes meeting above bases of antennae	Sciaridae (some females of *Bradysia* and *Epitapus*)*	p. 718
148′.	Eyes not meeting above bases of antennae	149*	
149(148′).	Palps 1-segmented; length about 2 mm	Sciaridae (females of *Pnyxia*)*	p. 718
149′.	Palps with 3 or more segments; length at least 4 mm	Mycetophilidae (females of *Baeopterogyna*, Yukon Territory and Alaska; and some *Boletina*, widely distributed)*	p. 718

150(142′).	Thorax very short, in dorsal view less than half as long as head, resembling abdominal segments; scutellum absent; parasitic on honey bee	Braulidae*	p. 740
150′.	Thorax at least as long as head, differing from abdominal segments; scutellum present; habits variable, but not parasitic on honey bees	151*	
151(150′).	Coxae widely separated (Figure 34–13A); abdominal segmentation sometimes obscure; tarsal claws toothed; ectoparasites of bats, birds, or mammals	Hippoboscidae*	p. 731
151′.	Coxae usually contiguous; abdominal segmentation distinct; tarsal claws simple; usually not ectoparasitic, but sometimes (Carnidae) associated with nestling birds	152*	
152(151′).	Frontal suture and frontal lunule present	153*	
152′.	Frontal suture and frontal lunule absent	160*	
153(152).	First segment of hind tarsi short and swollen, shorter than second segment (Figure 34–26A)	Sphaeroceridae*	p. 741
153′.	First segment of hind tarsi not swollen, longer than second segment	154*	
154(153′).	Propleuron with a vertical ridge	Chloropidae (some *Conioscinella*)*	p. 741
154′.	Propleuron without a vertical ridge	155*	
155(154′).	Face strongly convex	Ephydridae (some females of *Hyadina* and *Nastima*)*	p. 742
155′.	Face concave	156*	
156(155′).	Postverticals present; at least 2 pairs of fronto-orbitals	157*	
156′.	Postverticals absent; only 1 pair of fronto-orbitals	Opomyzidae (some *Geomyza*)*	p. 740
157(156).	Postverticals parallel or nearly so; gena with a pair of strong bristles in middle; associated with birds	Carnidae (*Carnus*)*	p. 741
157′.	Postverticals converging; gena without a row of strong bristles in middle; not associated with birds	158*	
158(157′).	Some or all tibiae with a preapical dorsal bristle; frons without strong fronto-orbitals on lower half	159*	
158′.	Tibiae without preapical dorsal bristles; frons with 2 pairs of strong fronto-orbitals on lower half	Anthomyzidae (some *Anthomyza*)*	p. 740
159(158).	Arista plumose; frons with a pair of proclinate fronto-orbitals	Drosophilidae (mutant *Drosophila*)*	p. 741
159′.	Arista bare or with short pubescence; no proclinate fronto-orbitals (some *Lutomyia*)	Heleomyzidae*	p. 741
160(152′).	Antennae apparently consisting of a single, globular segment with a 3-segmented arista; hind femora laterally flattened (some females)	Phoridae*	p. 727
160′.	Antennae with obviously 2 or 3 segments; arista, if present, 2-segmented; hind femora not flattened	161*	
161(160′).	Vertex convex; compound eyes bare; proboscis elongate and projecting	Empididae (*Chersodromia*)*	p. 725
161′.	Vertex excavated; compound eyes pubescent; proboscis short and retracted	Dolichopodidae (females of some *Campsicnemus*)*	p. 726

SUBORDER Nematocera—Long-Horned Flies: This suborder contains a little less than one third of the North American species of flies (nearly 5300), in 24 of the 108 families. Its members can be recognized by their many-segmented antennae, which are usually long. Most nematocerans are small, slender, and long-legged and are mosquito-like or midgelike in appearance. The wing venation varies from very complete (Tanyderidae) to greatly reduced (for example, the Cecidomyiidae). This suborder contains the only Diptera that have a 5-branched radius. The larvae, except in the Cecidomyiidae, have a well-developed head, with toothed or brushlike mandibles that move laterally. Most live in water or in moist habitats. The pupae are obtect.

The Nematocera are generally recognized to be a paraphyletic group, out of which the Brachycera arose. We continue to use the term Nematocera here because it remains commonly used in entomology.

This group contains many flies of considerable economic importance. Many are bloodsucking and serious pests of humans and animals (mosquitoes, punkies, black flies, and sand flies), and some of these serve as disease vectors. A few flies in this suborder (some Cecidomyiidae) are important pests of cultivated plants. The aquatic larvae of the Nematocera are an important food of many freshwater fishes.

***Family* Tipulidae—Crane Flies:** This family is the largest in the order, with approximately 1600 known species in North America. Many crane flies are common and locally abundant insects. They may be mistaken for large mosquitoes, but even those with elongate mouthparts cannot bite. A few are smaller than the smallest mosquitoes. The legs are usually long and slender (Figure 34–28) and are easily broken off. The body is usually elongate and slender, and the wings are long and narrow. Some crane flies are quite large: *Holorusia grandis* (Bergroth) of the western states, has a body length sometimes exceeding 35 mm and a wingspan of nearly 70 mm. Many species have clouded or patterned wings. Tipulids differ from Trichoceridae in lacking ocelli, from Tanyderidae in having four or fewer branches of the radius, and from Ptychopteridae in having two anal veins (Figure 34–7).

Crane flies live chiefly in damp habitats with abundant vegetation. There are, however, grassland species and even a few in deserts. Larvae of many species are aquatic or semiaquatic. Others live in the soil or in fungi, mosses, and decaying wood. Most eat decomposing plant matter, but certain aquatic groups are predaceous. Larvae of a few species feed on roots of young plants and if abundant may damage rangelands and seedling crops. Adult crane flies usually live only a few days, and probably most do not feed.

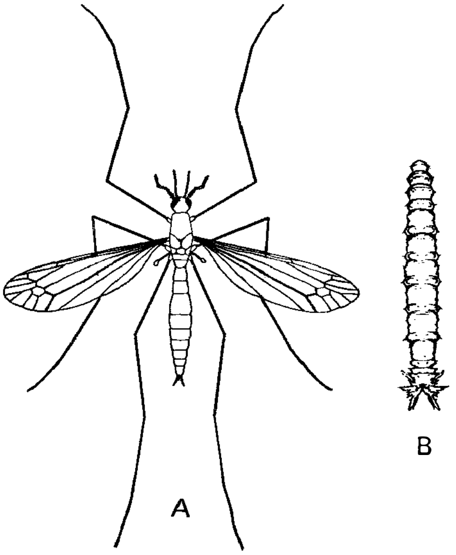

Figure 34–28 A crane fly (*Tipula* sp., family Tipulidae). A, adult; B, larva. (B, courtesy of Johannsen and the Cornell University Agricultural Experiment Station.)

British and American taxonomists have traditionally grouped the two subfamilies Cylindrotominae and Limoniinae together with this family. Most large crane flies belong to the Tipulinae. These are characterized by having the terminal segment of the maxillary palps slender and longer than the penultimate segment, and the antennae normally have 13 segments. The Limoniinae is a very large group of crane flies with nearly 1,000 species described from the United States and Canada. Nearly all small crane flies (but a few large ones and many of medium size) belong to the Limoniinae, in which veins R_1 and R_{2+3} are not fused (Figure 34–7D) and R_2 often has the form of a short crossvein between R_1 and R_3, or is absent. Their habits are very similar to the Tipulinae, with both aquatic and terrestrial forms. Typically, the larvae are found associated with decaying organic matter from plants and fungi. Small, wingless, spiderlike species of *Chionea* may be found on snow in winter. However, some with long, slender mouthparts (for example, subgenus *Geranomyia* of the large genus *Limonia*) take nectar from various flowers. The subfamily Cylindrotominae is a small group of crane flies, with only nine species recorded from North America. These are not commonly collected, but can be recognized by the fusion of veins R_1 and R_{2+3} well before the wing tip (Figure 34–7C). Larvae can be found in mosses or liverworts, or sometimes in leaves of higher plants.

***Family* Trichoceridae—Winter Crane Flies:** The trichocerids are medium-sized flies that resemble the crane flies in the family Tipulidae. They differ from the tipulids in having ocelli. They are usually seen in the fall or early spring, and some can be seen on mild days in winter. Adults can be found outdoors, sometimes in large swarms, or in caves, cellars, or similar dark places. The larvae live in decaying vegetable matter.

***Family* Psychodidae—Moth Flies and Sand Flies:** The psychodids are small to minute, usually very hairy, mothlike flies. The most common species (Psychodinae) hold the wings rooflike over the body. The adults live in moist, shady places, and they are sometimes abundant in drains or sewers. The larvae live in decaying vegetable matter, mud, moss, or water. The larvae of *Maruina* (Psychodinae), which occur in the West, live in fast-flowing streams.

This family is represented in the United States by 112 species, arranged in four subfamilies: Psychodinae, Trichomyiinae, Phlebotominae, and Bruchomyiinae. In the Psychodinae the eyes have a median extension extending above the base of the antennae. The other three subfamilies have the eyes oval, without a median extension. The Trichomyiinae differ from the Phlebotominae and Bruchomyiinae in Rs having three branches, with only one longitudinal vein between the two forked veins in the wing. In the Phlebotominae and Bruchomyiinae Rs has four branches, with two veins between the two forked veins in the wing (as in Figure 34–8G). The Phlebotominae differ from the Bruchomyiinae in having a long proboscis. Most North American psychodids (95 species) are in the subfamily Psychodinae. The Trichomyiinae contains only 3 species, the Phlebotominae 13, and the Bruchomyiinae only 1 (which occurs in Florida).

Most psychodids are harmless to humans, but those in the subfamily Phlebotominae, often called "sand flies," are bloodsucking. These occur in the southern states and in the tropics. Sand flies act as vectors of several diseases in various parts of the world: pappataci fever (caused by a virus) in the Mediterranean region and in southern Asia; kala-azar and oriental sore (caused by leishmania organisms), which occur in South America, northern Africa, and southern Asia; espundia (caused by a leishmania), which occurs in South America; and Oroya fever or verruga peruana (caused by a bartonella organism), which occurs in South America.

***Family* Ptychopteridae—Phantom Crane Flies:** These crane flies are similar to the tipulids, but they have only one anal vein reaching the wing margin and lack a closed discal cell. A fairly common species in this family, *Bittacomorpha clavipes* (Fabricius), has the long legs banded with black and white, and the basal segment of the tarsi is conspicuously swollen. These flies often drift with the wind, with their long legs extended. *Bittacomorpha* and *Bittacomorphella* have clear wings, and M_{1+2} is not forked (Figure 34–7A). In *Ptychoptera*, which resemble large fungus gnats, the wings are usually patterned, and M_{1+2} is forked. This is a small group, with only 16 North American species. The larvae live in decaying vegetable matter in marshes and swampy ponds.

***Family* Tanyderidae—Primitive Crane Flies:** This group is represented in North America by four species, of which one, *Protoplasa fitchii* Osten Sacken, occurs in the East. The tanyderids are medium-sized insects with banded wings, and their larval stages live in wet, sandy soil at the margins of large streams.

***Family* Ceratopogonidae—Biting Midges, Punkies, or No-see-ums:** These flies are very small but are often serious pests, particularly along the seashore or along the shores of rivers and lakes, because of their bloodsucking habits. Their small size is responsible for the name "no-see-ums," and their bite is out of all proportion to their size. Many species in this group attack other insects and suck blood from the insect host as an ectoparasite. Punkies have been reported from mantids, walkingsticks, dragonflies, alderflies, lacewings, certain beetles, certain moths, crane flies, and mosquitoes. Some of the larger species prey on smaller insects. Some species (Figure 34–29B) have spotted wings.

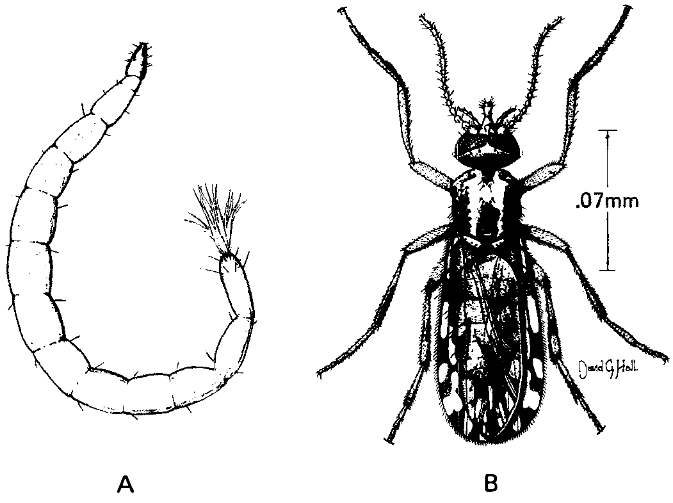

Figure 34–29 The little gray punkie, *Culicoides furens* (Poey) (Ceratopogonidae). A, larva; B, adult female; about 25×. (Courtesy of Dove, Hall, and Hull, and the Entomological Society of America.)

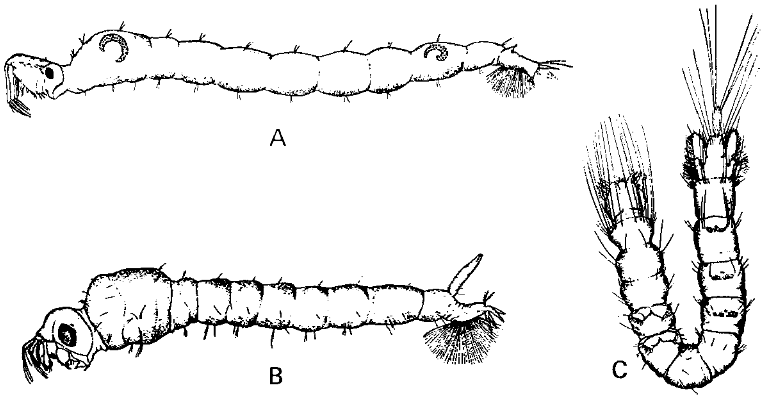

Figure 34–30 Larvae of phantom (A–B) and (C) dixid midges. A, *Chaoborus flavicans* (Meigen); B, *Mochlonyx cinctipes* (Coquillet); C, *Dixa aliciae* Johannsen. (Courtesy of Johannsen and the Cornell University Agricultural Experiment Station.)

Most punkies that attack people belong to the genera *Culicoides* and *Leptoconops*. These insects apparently do not travel far from the place where the larvae live, and one can often avoid punkie attacks by simply moving a few yards away.

Punkies are very similar to the midges (Chironomidae), but are generally stouter in build, with the wings broader and held flat over the abdomen (usually held more or less rooflike in the Chironomidae), and the wings are often strongly patterned (usually clear in Chironomidae). This large group has about 580 North American species.

The larvae of punkies are aquatic or semiaquatic, living in sand, mud, decaying vegetation, and the water in tree holes. Those living along the seashore apparently breed in the intertidal zone. The feeding habits of the larvae are not well known, but they are probably scavengers.

Family **Chaoboridae—Phantom Midges:** These insects are very similar to mosquitoes, but differ in having a short proboscis and fewer scales on the wings. They do not bite. The larvae (Figure 34–30A,B) are aquatic and predaceous, and their antennae are modified into prehensile organs. The larvae of *Chaoborus* (Figure 34–30A) are almost transparent, giving rise to the name "phantom midges" for this group. The larvae of some species (for example, *Mochlonyx*, Figure 34–30B) have a breathing tube and are very similar to mosquito larvae in appearance. Others (such as *Chaoborus*) do not have a breathing tube. The larvae live in various sorts of pools and are sometimes very abundant. They frequently destroy large numbers of mosquito larvae. The group is small (15 North American species), but its members are fairly common insects.

Family **Corethrellidae:** This is mainly a tropical group, with only five species in the United States and Canada. It is often classified within the Chaoboridae, from which it can be distinguished by the sparsely setose clypeus and by R_1 terminating away from the apex of the wing, closer to Sc than to R_2.

Family **Chironomidae—Midges:** These insects are almost everywhere. They are small (1–10 mm long), delicate, and somewhat mosquito-like in appearance (Figure 34–31C), but they lack scales on the wings, do not have a long proboscis (they do not bite), the front legs are usually the longest, and the metanotum has a keel or furrow. The males usually have plumose antennae. Midges often occur in huge swarms, usually in the

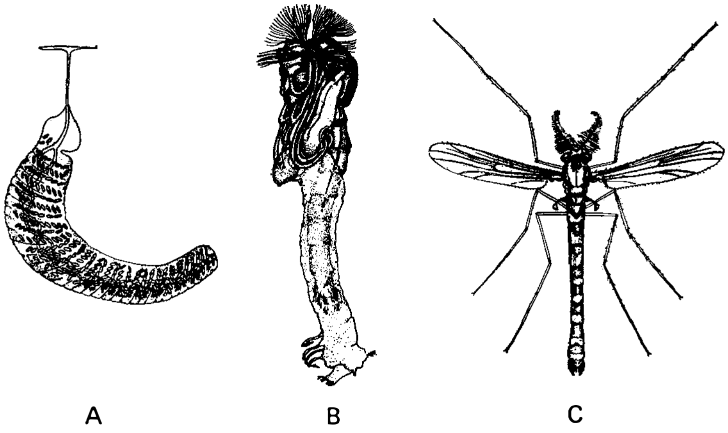

Figure 34–31 A midge, *Chironomus plumosus* (L.). A, egg mass; B, pupa, lateral view, with larval skin not completely shed; C, adult male. (Courtesy of Branch.)

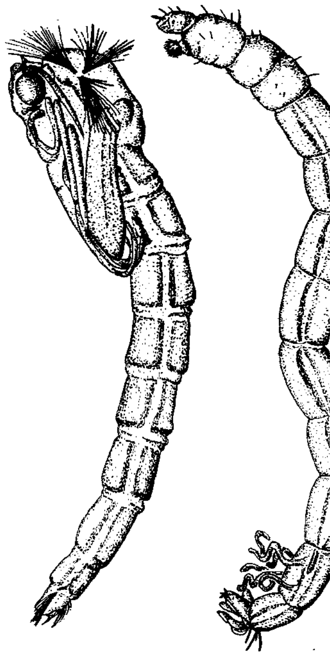

Figure 34–32 Pupa (A) and larva (B) of *Chironomus tentans* (Fabricius). (Courtesy of Johannsen and the Cornell University Agricultural Experiment Station.)

evening, and the humming of such a swarm can often be heard from a considerable distance.

This group is large, with about 1,090 North American species. The larvae of most midges (Figure 34–32B) are aquatic, and live in all sorts of aquatic habitats. Some live in decaying matter, soil, under bark, and similar habitats that are wet and rich in organic matter. Many of the aquatic forms live in tubes or cases that they make from fine particles of the substrate cemented together with salivary secretion. The larvae of many species are red (because hemoglobin is present in the hemolymph) and are known as bloodworms. Midge larvae swim by means of characteristic whipping movements of the body, something like the movements of mosquito larvae. Midge larvae are often very abundant, and are an important item of food for many freshwater fish and other aquatic animals.

Family **Culicidae—Mosquitoes:** This family is a large, abundant, well-known, and important group of flies. The larval stages are aquatic, and the adults can be recognized by the characteristic wing venation (Figure 34–81), the scales along the wing veins, and the long proboscis. Mosquitoes are very important from the standpoint of human welfare because the females are bloodsucking, many species bite people, and they serve as vectors in the transmission of several important and dangerous human diseases.

Mosquito larvae (Figure 34–33A,C), or wrigglers, live in a variety of aquatic situations—in ponds and pools of various sorts, in the water in artificial containers, in tree holes, and in other situations—but each species usually lives only in a particular type of aquatic habitat. The eggs (Figure 34–34) are laid on the surface of the water, either in "rafts" (*Culex*) or singly (*Anopheles*), or near water (*Aedes*). In the latter case the eggs usually hatch when flooded. The larvae of most species feed on algae and organic debris, but a few are predaceous and feed on other mosquito larvae. Mosquito larvae breathe principally at the surface, usually through a breathing tube at the posterior end of the body. The

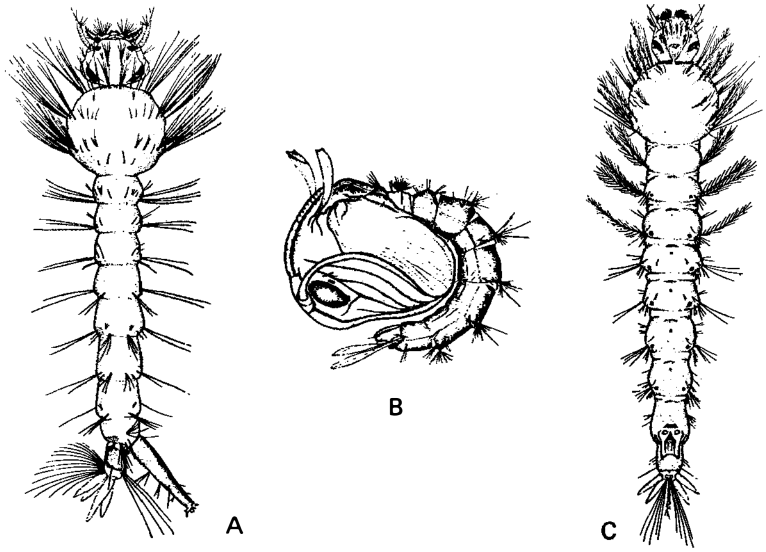

Figure 34–33 Larvae and pupa of mosquitoes. A, larva of *Culex pipiens* L.; B, pupa of *C. pipiens*; C, larva of *Anopheles punctipennis* (Say). (After Johannsen, courtesy of the Cornell University Agricultural Experiment Station.)

larvae of *Anopheles* lack a breathing tube and breathe through a pair of spiracular plates at the posterior end of the body.

Mosquito pupae (Figure 34–33B) are also aquatic and, unlike most insect pupae, are quite active and are often called tumblers. They breathe at the surface of the water through a pair of small, trumpetlike structures on the thorax.

Most adult mosquitoes do not travel far from the water in which they spent their larval stage. *Aedes aegypti* (L.), the vector of yellow fever and dengue, seldom travels more than a few hundred yards from where it emerges. Some species of *Anopheles* can range as far as a mile from where they emerge. In contrast, some of the salt-marsh mosquitoes—for example, *Aedes sollicitans* (Walker) (Figure 34–35A)—can be found many miles from the larval habitat. Adult mosquitoes usually

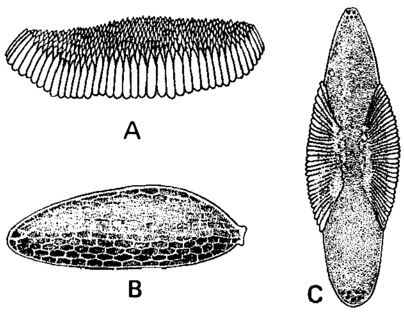

Figure 34–34 Eggs of mosquitoes. A, egg raft of *Culex restuans* Theobald; B, egg of *Aedes taeniorhynchus* (Wiedemann); C, egg of *Anopheles quadrimaculatus* Say, showing floats. (Courtesy of USDA, after Howard, Dyar, and Knab.)

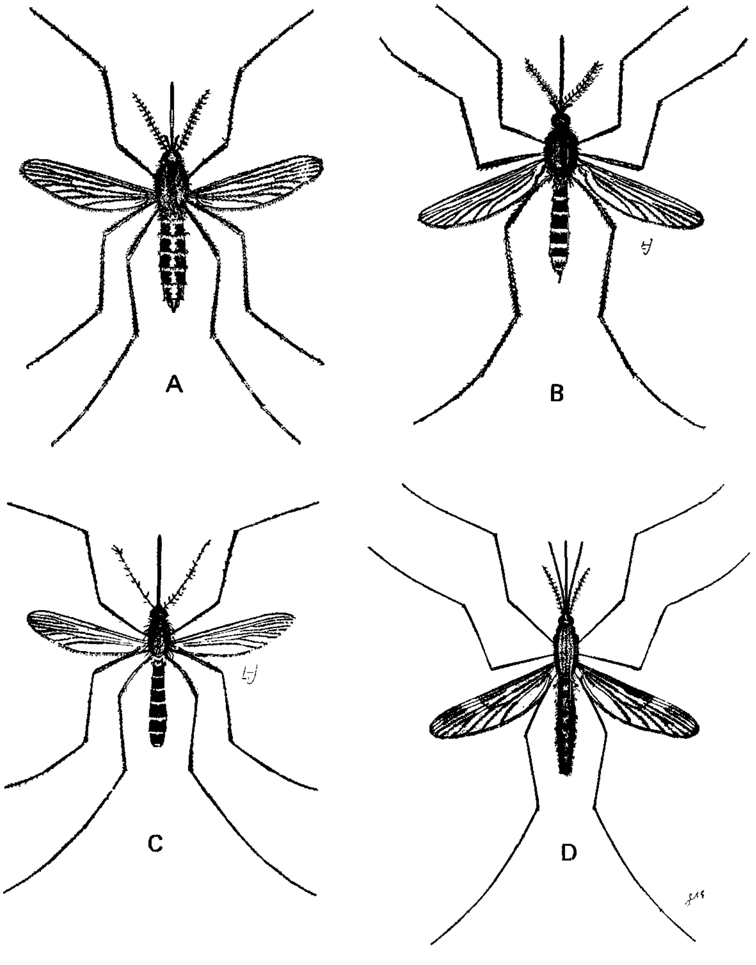

Figure 34–35 Common mosquitoes. A, the saltmarsh mosquito, *Aedes sollicitans* (Walker); B, a woodland mosquito, *Aedes stimulans* (Walker); C, the house mosquito, *Culex pipiens* L.; D, *Anopheles punctipennis* (Say). (Courtesy of Headlee and the New Jersey Agricultural Experiment Station.)

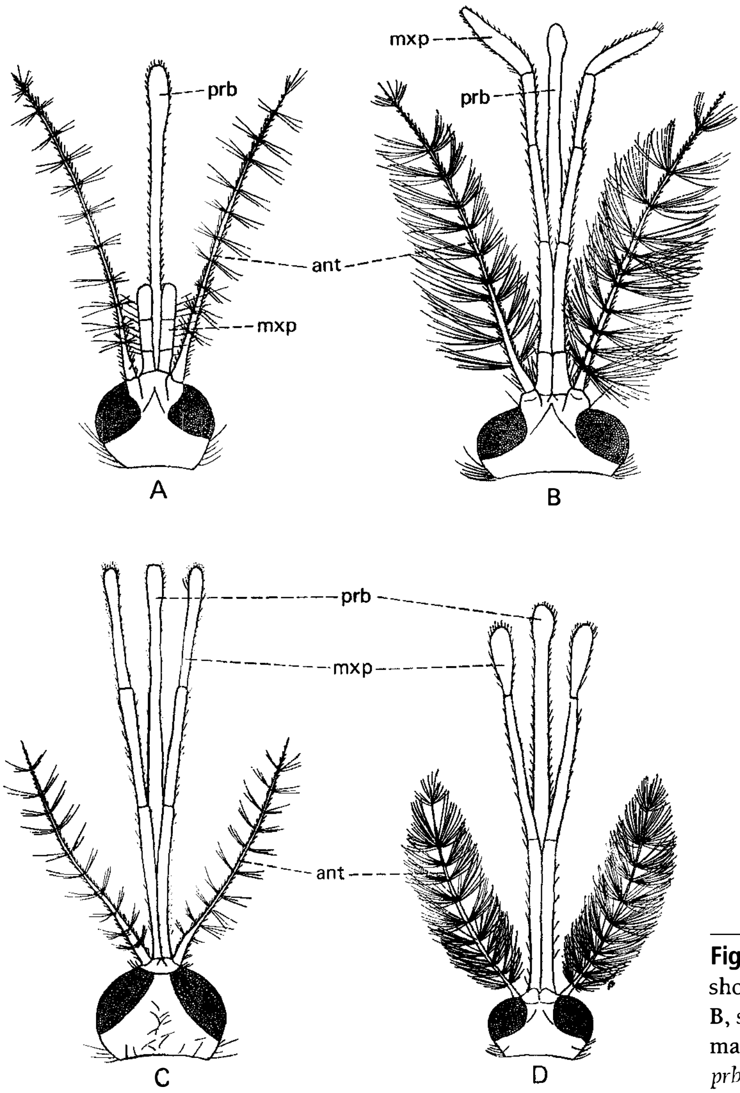

Figure 34–36 Head structure in mosquitoes, showing sex characters. A, *Aedes*, female; B, same, male; C, *Anopheles*, female; D, same, male. *ant*, antenna; *mxp*, maxillary palp; *prb*, proboscis.

are active during the twilight hours or at night, or in dense shade. Many spend the day in hollow trees, under culverts, or in similar resting places. Some adults overwinter in such places. Only the female mosquitoes are bloodsucking. The males (and occasionally also the females) feed on nectar and other plant juices.

The sexes of most mosquitoes can be easily determined by the form of the antennae (Figure 34–36). The antennae of the males are very plumose, whereas those of the females have only a few short hairs. In most mosquitoes other than *Anopheles* (see later), the maxillary palps are very short in the female (Figure 34–36A) but in the male are longer than the proboscis (Figure 34–36B).

Most of the mosquitoes discussed here (139 of the 166 species recorded from North America) belong to four genera: *Anopheles*, *Aedes*, *Psorophora*, and *Culex*. These genera contain the species that are most important from the human point of view. Adults of *Anopheles* are rather easily distinguished: the maxillary palps are long in both sexes (Figure 34–36C,D) and clubbed in the male (usually short in females of the other genera); the scutellum is evenly rounded (trilobed in the other genera); and the wings are usually spotted (not so in the other genera). The wing spotting in *Anopheles* is due to groups of differently colored scales on the wings. An *Anopheles* mosquito in a resting position holds the body and proboscis in a straight line and at an angle to the surface on which the insect is resting (Figure 34–37A,B). Some species seem almost to "stand on their head" in a resting position. Adults of the other genera hold the body in a resting position

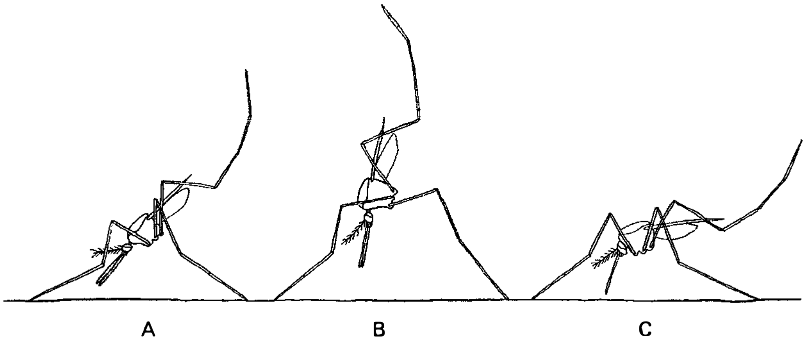

Figure 34–37 Resting positions of mosquitoes. A, B, *Anopheles*; C, *Culex* (Redrawn from King, Bradley, and McNeel.)

more or less parallel to the surface, with the proboscis bent down (Figure 34–37C). Adults of *Psorophora* have a group of bristles (the spiracular bristles) immediately in front of the mesothoracic spiracle, whereas those of *Aedes* and *Culex* lack spiracular bristles. *Psorophora* mosquitoes are relatively large and have long, erect scales on the hind tibiae. The best character to separate adults of *Aedes* and *Culex* is the presence (*Aedes*) or absence (*Culex*) of postspiracular bristles (a group of bristles immediately behind the mesothoracic spiracle). The tip of the abdomen of a female *Aedes* is usually pointed, with the cerci protruding, and the thorax often has white or silvery markings. In *Culex* the tip of the female abdomen is generally blunt, with the cerci retracted, and the color of the thorax is usually dull.

The larvae of *Anopheles* differ from those of other mosquitoes in lacking a breathing tube (Figure 34–33C), and at rest they lie parallel to the surface of the water (Figure 34–38A). The larvae of the other three genera have a breathing tube (Figure 34–33A), and at rest they hold the body at an angle to the surface of the water (Figure 34–38B). *Culex* larvae have several pairs of hair tufts on the breathing tube, and the tube is relatively long and slender. Larvae of *Aedes* and *Psorophora* have only a single pair of hair tufts on the breathing tube. The larvae of *Aedes* and *Psorophora* usually differ in the sclerotization of the anal segment (the sclerotization going completely around the segment in *Psorophora* but usually not complete in *Aedes*). The breathing tube in *Aedes* larvae is relatively short and stout.

Anopheles larvae live chiefly in ground pools, marshes, and places where there is considerable vegetation. The other mosquitoes breed in many places, but the most abundant *Aedes* and *Psorophora* mosquitoes breed in woodland pools and salt marshes, and *Culex* in artificial containers. The woodland species that are so troublesome early in the season are largely species of *Aedes* and have a single brood a year. Many species that breed in large bodies of water, borrow pits, or artificial containers can continue breeding through the season as long as weather conditions are favorable.

Mosquitoes act as vectors of several very human important diseases: malaria, caused by protists of the genus *Plasmodium* and transmitted by certain species of *Anopheles*; yellow fever, caused by a virus and trans-

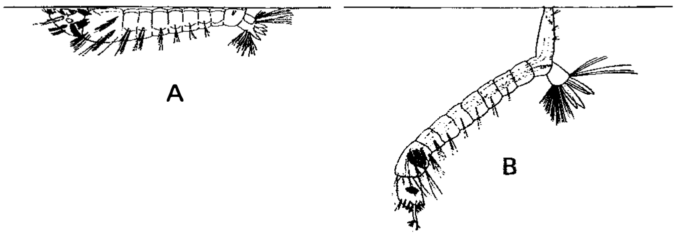

Figure 34–38 Feeding positions of mosquito larvae. A, *Anopheles*; B, *Culex*. (Courtesy of USDA.)

mitted by *Aedes aegypti* (L.); dengue, caused by a virus and transmitted by *Aedes aegypti* (L.) and other species of *Aedes*; filariasis, caused by a filarial worm (Nematoda) and transmitted chiefly by species of *Culex*; and certain types of encephalitis, caused by a virus and transmitted by various species of mosquitoes (chiefly species of *Culex* and *Aedes*). The recently introduced West Nile fever is caused by a virus and transmitted by a wide variety of mosquitoes, primarily species in the genus *Culex*, that have fed on infected birds.

Control measures against mosquitoes can be aimed at the larvae or at the adults. Measures aimed at the larvae can involve eliminating or modifying the larval habitats (for example, drainage) or treating the larval habitat with insecticides. Measures aimed at the adults may be preventives (protective clothing, screening, and the repellents) or insecticides (sprays or aerosols).

Family **Dixidae**: The dixids are small, slender, mosquito-like flies with long legs and antennae. The wings lack scales, and the base of R_{2+3} is somewhat arched (Figure 34–8H). The adults do not bite. The larvae (Figure 34–30C) are aquatic and somewhat similar to the larvae of *Anopheles* mosquitoes, but do not have an enlarged thorax (cf. Figure 34–33C). They feed at the surface of the water like anopheline larvae, but the usual position is with the body bent into a U, and they move by alternately straightening and bending the body. The larvae feed on microorganisms and decayed organic matter. The group is a small one (45 North American species), but its members are fairly common.

Family **Simuliidae—Black Flies or Buffalo Gnats**: The black flies are small, usually dark-colored insects with short legs, broad wings, and a humpbacked appearance (Figure 34–39). The females are bloodsucking. These insects are vicious biters and are serious pests in some sections of the country. The bites often cause considerable swelling and sometimes bleeding. Black flies sometimes attack livestock in such numbers and with such ferocity as to cause the death of the livestock, and there are records of human deaths caused by these insects. Black flies are represented by approximately 165 species; they have a wide distribution, but are most numerous in the north temperate and subarctic regions. The adults usually appear in late spring and early summer.

Black fly larvae live in streams, where they attach to stones and other objects by means of a disclike sucker at the posterior end of the body. The larvae (Figure 34–40C,G) are somewhat club-shaped, are swollen posteriorly, and move about like a measuringworm. Their locomotion is aided by silk spun from the mouth. They pupate in cone-shaped cases (Figure 34–40B,E) attached to objects in the water. These larvae are sometimes extremely abundant. The adults are most frequently encountered near the streams where the larvae live, but may live at considerable distances from streams.

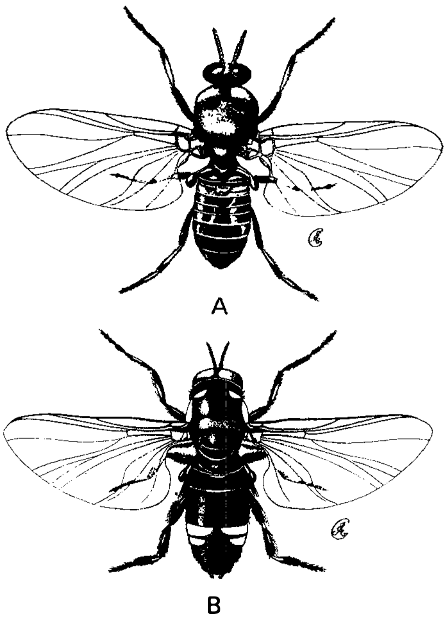

Figure 34–39 A black fly, *Simulium nigricoxum* Stone. A, female; B, male. (Courtesy of Cameron and the Canadian Department of Agriculture.)

The black flies in the United States are not known to be vectors of any disease of humans, but in Africa, Mexico, and Central America certain species in this group act as vectors of onchocerciasis, a disease caused by a filarial worm (Nematoda) and characterized by large subcutaneous swellings. In some cases the worms get into the eyes and cause partial or complete blindness.

Family **Thaumaleidae**: The members of this family are small (3–4 mm long), rather stocky flies with the head situated low on the thorax, and reddish yellow or brownish. Twenty-four species occur in the United States, three in the East and the others in the West. They are quite rare. The adults are usually found along streams in which the larvae live.

Family **Blephariceridae—Net-Winged Midges**: These insects are long-legged, mosquito-like or tipulid-like insects, 3–13 mm long. They differ from the crane flies (Tipulidae) in lacking the V-shaped suture on the mesonotum. They sometimes have a network of fine lines between the wing veins, the anal angle of the wing is well developed, and the base of M_3 is lacking (Figure 34–8J). The adults are found near fast-flowing streams but are not common. The larvae live in swift

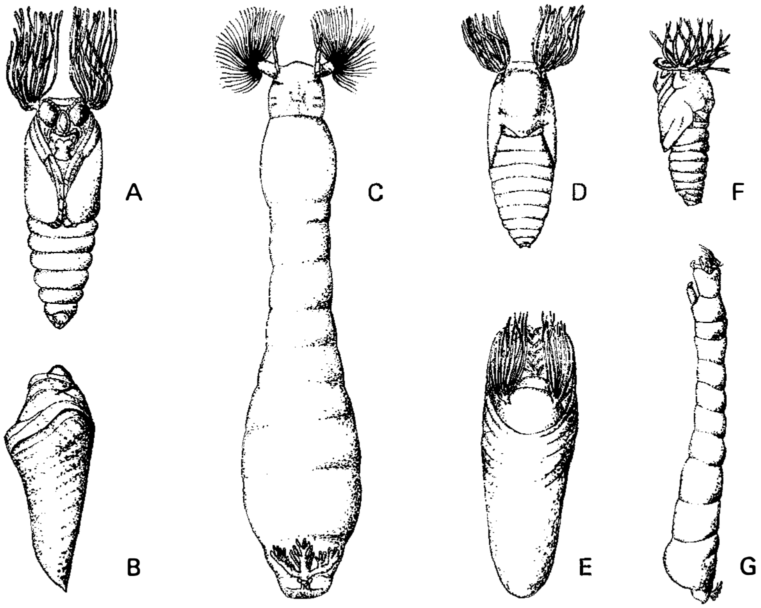

Figure 34–40 Immature stages of a black fly. A–E, *Simulium nigricoxum* Stone; F–G, *S. pictipes* Hagen. A, pupa, ventral view; B, pupal case; C, larva, dorsal view; D, pupa, dorsal view; E, pupa in pupal case; F, pupa, lateral view; G, larva, lateral view. (A–E, courtesy of Cameron and the Canadian Department of Agriculture; F–G, courtesy of Johannsen and the Cornell University Agricultural Experiment Station.)

water, clinging to rocks by means of a series of ventral suckers.

***Family* Deuterophlebiidae—Mountain Midges:** These midges are peculiar in having broad, fanlike wings, and the males have extremely long antennae (about four times as long as the body). Six species of *Deuterophlebia* are known from the West (Colorado to California, north to Alberta), where the larvae live in swift-flowing streams.

***Family* Nymphomyiidae:** Two species are known from the Nearctic region, *Nymphomyia dolichopeza* Courtney, from the southern Appalachians of Georgia, North Carolina and South Carolina; and *Nymphomyia walkeri* (Ide), which has been collected in streams from Quebec and New Brunswick to Alabama. The species are characteristically found in pristine mountain streams, with the larvae living on stones and among aquatic mosses and other vegetation. During oviposition, the copulating male and female crawl underwater to an oviposition site. While there, the wings are often broken off, but the mechanism for this is unknown. The only other known species in the family are found in east Asia from India to Japan and the Russian Far East.

***Family* Anisopodidae—Wood Gnats:** This is a small group of gnats (nine North American species) that are usually found in moist places on foliage. Some species occasionally live in large swarms consisting entirely of males. The larvae live in or near decaying organic matter, fermenting sap, and similar materials, and the adults are often attracted to flowing sap. Two subfamilies occur in North America, the Mycetobiinae and Anisopodinae. The Mycetobiinae lack a discal cell, and the two basal cells are confluent because of the absence of the base of M (Figure 34–9C). The Anisopodinae have a discal cell, and the two basal cells are separated by the base of M (Figure 34–8B). The Mycetobiinae contains a single, rare, but widely distributed species, *Mycetobia divergens* Walker. The most commonly encountered wood gnats are members of the Anisopodinae, which often have faint spots on the wings.

***Family* Axymyiidae:** This family includes two North American species, *Axymyia furcata* McAtee, which occurs in the East, and another species of *Axymyia* that has been found in Oregon. These are medium-sized, stout-bodied flies, resembling some of the march flies (*Bibio*) in appearance, with short antennae and characteristic wing venation (Figure 34–9D). The larvae live in cavities in moist, rotting wood. These insects are relatively rare, and little is known of the habits of the adults.

***Family* Bibionidae—March Flies:** The march flies are small to medium-sized, usually dark-colored, hairy or bristly flies, with short antennae that arise low on the face (Figure 34–41). Many have a red or yellow thorax. The wings often have a dark spot near the end of R_1 (Figure 34–8C). The adults are most common in spring and early summer, and are sometimes abundant. The larvae live in decaying organic matter and among plant roots.

One member of this family, *Plecia nearctica* Hardy (Figure 34–41), which occurs in the Gulf States, sometimes (usually in May and September) congregates in enormous swarms. Cars driving through such swarms

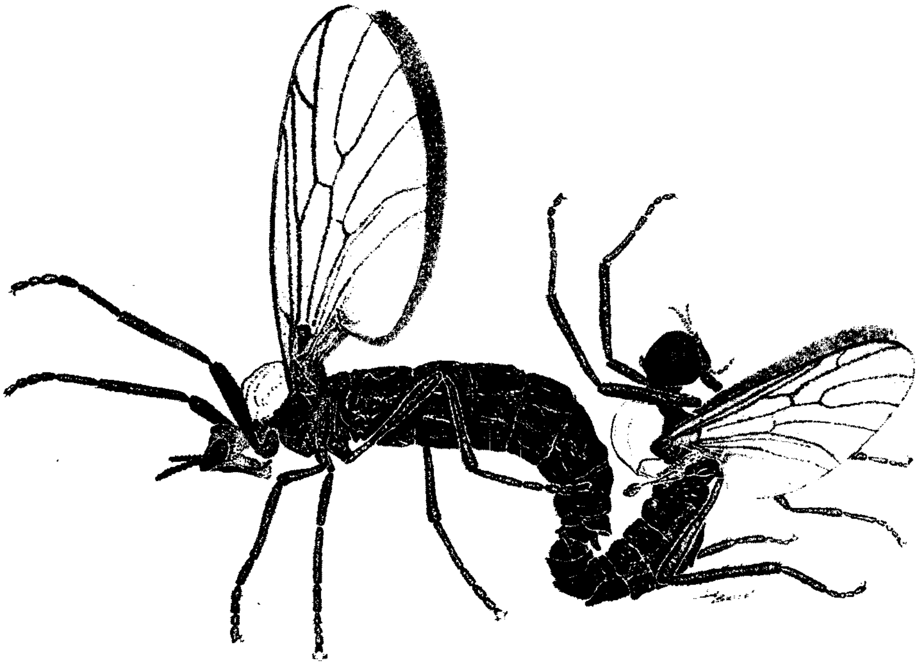

Figure 34–41 A mating pair of "lovebugs," *Plecia nearctica* Hardy, a species of march fly. (Courtesy of Dwight Bennett.)

become spattered with these flies, which can clog radiator fans and cause the car to overheat, or spatter the windshield and obscure the driver's vision. If they are not soon cleaned off, they may damage the car's finish. Because pairs are often seen in copulo, these insects are commonly called "lovebugs." They are a particular problem in the northern part of peninsular Florida and in other Gulf states.

The subfamily Hesperininae is represented in North America by only a single species, *Hesperinus brevifrons* Walker. It is recorded from Alaska, Canada, and the western and northeastern United States. Some entomologists recognize the subfamily as a separate family, and it can be distinguished by the elongate antennae and the branched Rs.

Family **Canthyloscelididae:** These rare flies are similar to the Scatopsidae. They differ in having the four-segmented palps (one-segmented in the Scatopsidae). The larvae live in decaying wood. Two species occur in North America. They have been collected from Quebec to California and north to Alaska.

Family **Cecidomyiidae—Gall Midges** or **Gall Gnats:** The gall midges are small (mostly 1–5 mm long), delicate flies with long legs and usually long antennae and with a reduced wing venation (Figures 34–8A, 34–42, 34–43A). This group is a large one, with some 1,200 North American species, about two thirds of which are gall makers. Larvae of the others feed on plant (without producing galls) or live in decaying vegetation or wood, or in fungi. A few are predaceous on other small insects.

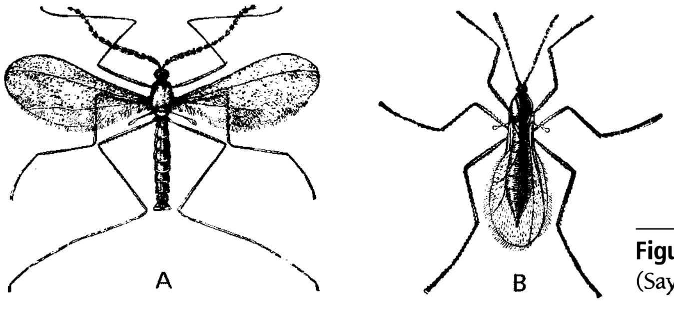

Figure 34–42 The Hessian fly, *Mayetiola destructor* (Say). A, male; B, female. (Courtesy of USDA.)

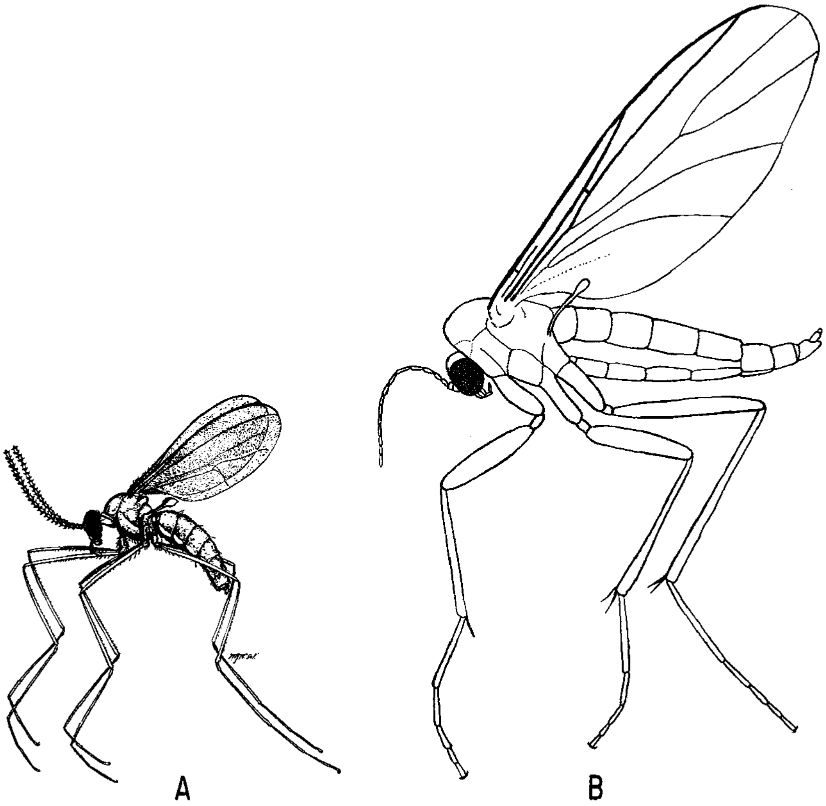

Figure 34–43 A, a cecidomyiid, *Aphidolestes meridionalis* Felt (which is predaceous on aphids); B, a dark-winged fungus gnat, *Sciara* sp., 15×. (A, courtesy of USDA.)

The larvae of gall midges are tiny maggots, with a small and poorly developed head and minute mouthparts. The last larval instar of most species has a characteristic T-shaped or clove-shaped sclerite on the ventral side of the prothorax called the "breastbone" or "sternal spatula." Many of the larvae are brightly colored—red, orange, pink, or yellow.

The galls formed by gall midges live on all parts of plants and are usually very distinctive. Many species of gall midges form a characteristic gall on a particular part of a particular species of plant. In some galls, such as the pine-cone willow gall and the maple leaf spot (Figure 34–44), only one larva develops. In others, such as the stem gall of willow, many larvae develop.

Paedogenesis (reproduction by larvae) occurs in several genera of gall midges. In *Miastor metraloas* Meinert, the larvae of which live under bark, daughter larvae are produced inside a mother larva, and they eventually consume it and escape. These larvae may produce more larvae in a similar manner, through several generations, and the last larvae pupate.

One of the most important pest species in this group is the Hessian fly, *Mayetiola destructor* (Say), which is a serious pest of wheat (Figure 34–42). This insect overwinters as a full-grown larva in a puparium, under the leaf sheaths of winter wheat. The larvae pupate and the adults emerge in the spring. These adults oviposit on wheat, and the larvae feed between the leaf sheath and the stem, weakening the shoot or even killing it. The larvae pass the summer in a puparium, and the adults emerge in the fall and lay their eggs on

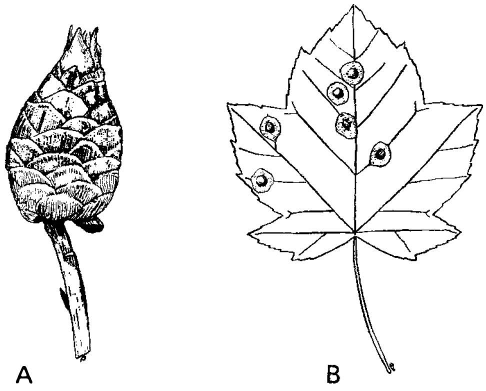

Figure 34–44 Galls of cecidomyiids. A, the pine-cone willow gall, caused by *Rhabdophaga strobiloides* (Osten Sacken); B, the maple leaf spot, caused by *Cecidomyia ocellaris* Osten Sacken. (Redrawn from Felt.)

the leaves of winter wheat. The damage to winter wheat can often be avoided by delaying the planting of wheat so that by the time the wheat has sprouted, the adult Hessian flies have emerged and died.

Other species of economic importance in this family are the clover flower midge, *Dasineura leguminicola* (Lintner), which is a serious pest of red clover throughout the United States; the chrysanthemum gall midge, *Rhopalomyia chrysanthemi* (Ahlberg), a pest of chrysanthemums grown in greenhouses in various parts of the country; and the alfalfa gall midge, *Asphondylia websteri* Felt, which is sometimes a serious pest of alfalfa in the Southwest.

North American gall midges are grouped in three subfamilies, the Lestremiinae, Porricondylinae, and Cecidomyiinae. The Lestremiinae usually have ocelli; the basal tarsal segment longer than the second; and M_{1+2} is present. The other two subfamilies lack ocelli and usually also M_{1+2}, and the first tarsal segment is much shorter than the second or the tarsi have fewer than five segments. In the Cecidomyiinae, h the basal section of Rs is very weak or lacking, whereas in the Porricondylinae the basal section of Rs is present and as strong as the other veins. The gall-making cecidomyiids are in the subfamily Cecidomyiinae. The larvae of the other two subfamilies live in decaying vegetation or wood, in fungi, or in plant tissues without producing galls. The larvae of some of the Cecidomyiinae also live in fungi or in plant tissues without producing galls, and a few are predaceous.

The subfamily Lestremiinae includes *Baeonotus microps* Byers, which was originally placed in a family by itself, the Baeonotidae. This species lacks wings, halteres, and ocelli; the compound eyes are single-faceted; and the abdomen is large and indistinctly segmented. This insect was collected in forest soil, beneath oak leaf litter, in Virginia.

Family **Mycetophilidae**—Fungus Gnats: The fungus gnats are slender, mosquito-like insects with elongated coxae and long legs (Figure 34–45). They are usually found in damp places where there is an abundance of decaying vegetation or fungi. The group is a large one, with more than 700 described North American species, and many of its members are common insects. Most fungus gnats are about the size of mosquitoes, but a few are 13 mm or more long. The larvae of most species live in fungi, moist soil, or decaying vegetation. Some species are pests in mushroom cellars. The larvae of the Keroplatinae spin mucous webs. Some of these are fungus feeders, and others are predaceous. Some of the predaceous larvae, such as *Orfelia fultoni* (Fisher) (Figure 34–45), are luminescent. Some adults of the Keroplatinae, including some of the largest North American fungus gnats, feed on flowers.

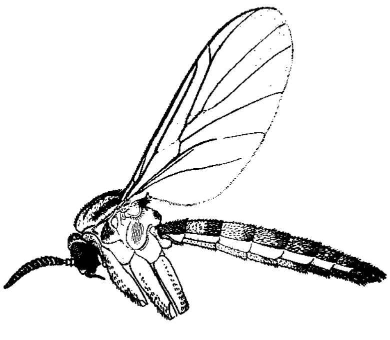

Figure 34–45 A fungus gnat, *Orfelia fultoni* (Fisher), 8×. (Courtesy of Fulton and the Entomological Society of America.)

The recognition of the Sciaridae as a separate family renders the Mycetophilidae a paraphyletic group. As such, the current subfamilies—Ditomyiinae (6 species in two genera), Diadocidiinae (4 species in one genus), Bolitophilinae (20 species in one genus), Lygistorrhininae (1 species), Manotinae (1 species) and Keroplatinae (82 species in twelve genera)—should probably be recognized at the level of family.

Family **Pachyneuridae:** This group includes a single North American species, *Cramptonomyia spenceri* Alexander, which occurs in the Northwest (Oregon, Washington, and British Columbia). This is a medium-sized, long-legged, slender, tipulid-like fly. The wings have a crossvein between the branches of Rs, a closed discal cell, and a dark spot near the end of R_1, and the antennae are slender and about as long as the head and thorax combined. This is a rare fly, and its immature stages are unknown. The larvae of other genera in the family live in rotten wood.

Family **Scatopsidae**—Minute Black Scavenger Flies: These flies are black or brownish, usually 3 mm long or less, and have short antennae. The veins near the costal margin of the wing (C, R_1, and Rs) are heavy, whereas the remaining veins are quite weak, and Rs ends at about one half to three fourths the wing length (Figure 34–9B). The larvae breed in decaying material and excrement. The group is a small one (76 North American species), but its members are sometimes fairly abundant.

Family **Sciaridae**—Dark-Winged Fungus Gnats, Root Gnats: These gnats are closely related and similar to the Mycetophilidae (Figure 34–43B), but have the eyes meeting above the bases of the antennae (Figure 34–9A) (except in *Pnyxia*), and the r-m crossvein is in line with and appears as a basal extension of Rs (Figure 34–10C,D). The sciarids are usually blackish insects and generally live in moist, shady places. The larvae of most species live in fungi, and some occasionally become pests in mushroom cellars. The larvae of a few species attack the roots of plants. One species, the potato scab gnat, *Pnyxia scabiei* (Hopkins), attacks potatoes and serves as the vector of potato scab. The females of *P. scabiei* have extremely short wings and no halteres. Sciarids are fairly common insects, with 170 species known from the United States and Canada.

SUBORDER Brachycera: This suborder includes 79 of the 104 families and nearly 14,000 of the approximately 20,000 known species of North American Diptera. Most of its members are relatively stout-bodied, and they vary greatly in size. The antennae usually have three segments, but the third segment is sometimes divided into subsegments, and it often bears a style or an arista.

The suborder Brachycera is divided into four infraorders, the Xylophagomorpha, Stratiomyomorpha, Tabanomorpha, and Muscomorpha. Some classifications of the Diptera limit the suborder Brachycera to the 19 families in the Xylophagomorpha, Stratiomyomorpha, Tabanomorpha, and the superfamilies Nemestrinoidea, Asiloidea, and Empidoidea; the remaining 60 families of Muscomorpha are then grouped in a third suborder, the Cyclorrhapha. Here the Cyclorrhapha are treated as a monophyletic group within the Muscomorpha. All the Cyclorrhapa have two-branched Rs, none has an annulated third antennal segment, and nearly all have an arista on the third antennal segment. The remaining Brachycera (except the Dolichopodidae, many Empididae, and some Stratiomyidae, Bombyliidae, and Acroceridae) have three-branched Rs, with R_{4+5} forked (in few Asilidae it may appear that R_{2+3} is forked; see Figure 34–11D).

The pupae of Brachycera are coarctate. In the groups outside of the Cyclorrhapa, the adult emerges from a T-shaped opening at one end. In the Cyclorrhapa the adult emerges from a circular opening at one end (hence the name), and the members of this group are often called "circular-seamed flies." Adults push out the end of the puparium with a structure called the *ptilinum*, a sac that is everted from the front of the head, above the bases of the antennae. After emergence, the ptilinum is withdrawn into the head. In the Calyptratae and Acalyptratae (a monophyletic group called the Schizophora), the break in the head wall through which the ptilinum was everted is marked by the frontal suture (also called the *ptilinal suture*). This suture is lacking in the Aschiza, itself probably a paraphyletic group.

***Family* Xylophagidae:** Xylophagids are relatively uncommon flies of medium to large size. They are black, sometimes marked with yellow, or all reddish yellow. They usually live in wooded areas, and feed on sap or nectar. The larvae live in the soil (*Coenomyia*), under bark (*Xylophagus*), or in decaying logs (*Rachicerus*). The flies in the genus *Xylophagus* are slender and ichneumonidlike, but other xylophagids are more robust. *Coenomyia ferruginea* (Scopoli) is large (14–25 mm long) and usually reddish or brownish, with the eyes pubescent and the second to fifth posterior cells about as wide as long (Figure 34–12B). The flies in the genus *Rachicerus* are peculiar in having the antennae many-segmented and serrate or somewhat pectinate. The fourth posterior (M_3) cell is closed, the eyes are emarginate just above the antennae, and these insects are 5–8 mm long. Other xylophagids are 10 mm long or less, and are quite rare.

***Family* Stratiomyidae—Soldier Flies:** This is a fairly large group (more than 260 known North American species), most of which are medium-sized or larger (to about 18 mm long) and usually found on flowers. Many species are brightly colored and wasplike in appearance. The larvae live in a variety of situations: Some are aquatic and feed on algae, decaying materials, or small aquatic animals; some live in dung or other decaying materials, some live under bark, and others are found in other situations.

In some species of soldier flies (for example, *Stratiomys*, Figure 34–46A), the abdomen is broad and flat; the wings at rest are folded back together over the abdomen; and the antennae (Figure 34–1C) are long, with the third segment distinctly annulated. In other species (such as those in the genus *Ptecticus*), the abdomen is elongate, usually narrowed at the base; and the third antennal segment (Figure 34–1F) appears globular, with an arista, and the annulations are very indistinct. Most soldier flies are dark-colored, with or without light markings, but some species are yellowish or light brown. The members of this family are most easily recognized by their wing venation: The branches of R are rather heavy and are crowded together in the anterior part of the wing, the wing membrane beyond the closed cells has fine, longitudinal wrinkles, and the discal cell is small (Figure 34–11A).

***Family* Xylomyidae:** These are rather slender, wasplike flies, 5–15 mm long, rather brightly colored with pale markings on blackish background. The most common flies in this small group (11 North American species) are the species of *Xylomyia*, which are slender and ichneumonidlike. They differ from xylophagids in the genus *Xylophagus* (which are very similar in appearance) in having the M_3 cell closed (Figure 34–12C). The xylomyids are usually found in wooded areas. The larvae live under bark, and are predaceous or scavengers.

***Family* Athericidae:** These flies were formerly placed in the Rhagionidae, but differ from those in that family in lacking spurs on the front tibiae and in having the R_1 cell closed at the wing margin (Figure 34–12D). This

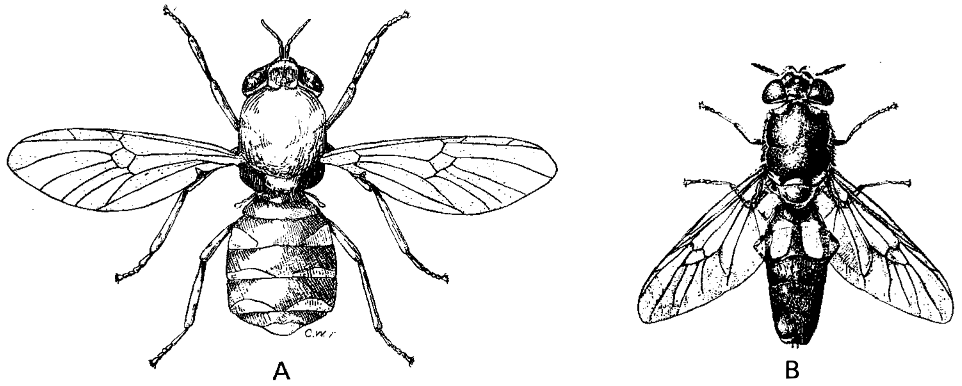

Figure 34–46 Soldier flies. A, *Stratiomys laticeps* Loew; B, *Hermatia illucens* (L.). (B, courtesy of USDA.)

group is a small one, with only five North American species, and its members are not common. They are usually found in the vegetation bordering streams. The eggs are usually laid on the underside of bridges or on vegetation above a stream, and the larvae on hatching fall into the stream, where they live in the riffles and feed on midge larvae and other aquatic insects. In the case of *Atherix* (widely distributed), the female remains on her egg mass and eventually dies there, and other females may lay eggs on this same mass until a ball of considerable size is formed—consisting of eggs and dead females. Females of *Suragina concinna* (Williston), which occurs in southwest Texas and Mexico, are bloodsucking, feeding on people and cattle.

***Family* Pelecorhynchidae:** This group includes eight rare North American species: seven species of *Glutops* and one species of *Pseudoerinna*. The species of *Glutops* are shorter than 10 mm, and have R_4 and 2A relatively straight; *Pseudoerinna jonesi* (Cresson) is 13–15 mm long, and has R_4 and 2A somewhat sinuate. A few species of *Glutops* occur in the East, but the other species in the family are western. The larvae live in the wet soil of swamps and stream banks, and are predaceous; the adults of a few species feed on flowers.

***Family* Rhagionidae—Snipe Flies:** Snipe flies are medium-sized to large, with the head somewhat rounded, the abdomen relatively long and tapering, and the legs rather long (Figure 34–47). Many species have spotted wings. The body may be bare or covered with short hair. Most snipe flies are brownish or gray, but some are black with spots of white, yellow, or green. They are common in woods, especially near moist places, and are usually found on foliage. Both adults and larvae are predaceous on a variety of small insects. Most snipe flies do not bite, but several species of *Symphoromyia* are common biting pests in the western mountains and coastal areas.

This group includes the genus *Bolbomyia*, which is sometimes placed in the Xylophagidae. It is a minute fly, 2–3 mm long, dull black with smoky wings, and with characteristic antennae (see couplet 40 of key). Some other genera, formerly included in the Rhagionidae, are placed in other families: *Atherix* in the family Athericidae, *Vermileo* in the family Vermileonidae, and *Dialysis* in the family Xylophagidae.

***Family* Tabanidae—Horse Flies and Deer Flies:** About 350 species of tabanids occur in North America, and many are quite common. They are medium-sized to large, rather stout-bodied flies. The females are bloodsucking and are often serious pests of livestock and people. The males feed chiefly on pollen and nectar and are often found on flowers. The two sexes are very easily separated by the eyes, which are contiguous in the males and separated in the females. The eyes are often brightly colored or iridescent. The larvae of most species are aquatic and predaceous, and the adults are generally encountered near swamps, marshes, ponds, and other situations where the larvae live. Most horse flies are powerful fliers, and some species apparently have a flight range of several kilometers.

The two most common genera of tabanids, which include some 180 of the 317 North American species, are *Tabanus* and *Chrysops*. In *Tabanus* the hind tibiae lack apical spurs, the head is somewhat hemispherical (slightly concave posteriorly in the female), and the third antennal segment (Figure 34–48A) has a toothlike process near the base. *Tabanus* is a large genus, with about a hundred North American species, and

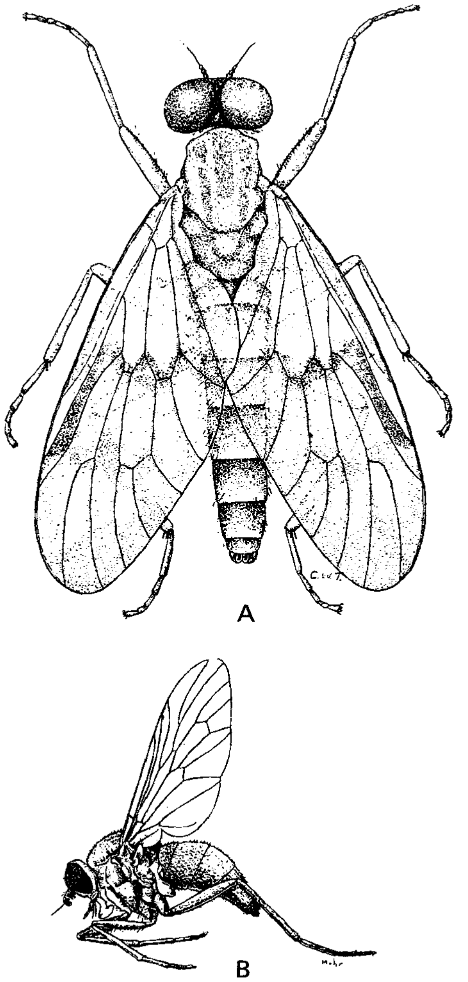

Figure 34–47 Snipe flies. A, a common snipe fly, *Rhagio mystaceus* (Macquart); B, a blood-sucking snipe fly, *Symphoromyia atripes* Bigot. (B, courtesy of Ross and the Entomological Society of America.)

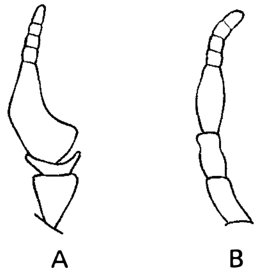

Figure 34–48 Antennae of tabanids. A, *Tabanus atratus* Fabricius; B, *Chrysops fuliginosus* Wiedemann.

it includes some important pests. One of the largest flies in the genus is *T. atratus* Fabricius, a black insect 25 mm or more long (Figure 34--49E). The so-called greenheads, flies about 13 mm long, with green eyes and a yellowish brown body, are often serious pests on bathing beaches. In *Chrysops* the hind tibiae have apical spurs, the head is more rounded, the calypteres are smaller, and the third antennal segment (Figure 34–48B) is elongate and lacks a toothlike basal process. Most members of this genus are about the size of a house fly or a little larger, brown or black, with dark markings on the wings (Figure 34--49A,B). These tabanids, called *deer flies*, are usually encountered near marshes or streams, and they frequently buzz around one's head or get in one's hair.

The eggs of tabanids are usually laid in masses on leaves or other objects near or over water. Most species overwinter in the larval stage and pupate during the summer. *Goniops chrysocoma* Osten Sacken is often found in forests; the female remains with her egg mass, guarding them until they hatch.

Some of the tabanids, particularly certain species of *Chrysops*, serve as vectors of disease. Tularemia and anthrax (and possibly other diseases) can be transmitted by tabanids in the United States, and in Africa a disease caused by the filarial worm *Loa loa* (Cobbold) is transmitted by deer flies.

Family **Vermileonidae—Worm Lions**: This group includes small (about 5 mm long), slender, nearly bare flies with stylate antennae, slender legs, and a long, slender abdomen. The wings are narrowed at the base, without an alula or a developed anal angle. The larvae of these flies construct pitfall traps in the sand, and they use these in capturing prey (very much as antlions do; see Chapter 27). The adults feed on nectar. Only two species, in the genus *Vermileo*, occur in the United States, from Colorado to New Mexico to California. The vermileonids are similar to the Rhagionidae, with which they were once classified, but differ in having the wings more narrowed at the base and in having apical spurs on the front tibiae.

Family **Acroceridae—Small-Headed Flies**: These are rather rare flies of small to medium size with a somewhat humpbacked appearance and with a very small head (Figure 34–50). Some have a long, slender proboscis and feed on flowers. Others have no proboscis and apparently do not feed in the adult stage. The larvae are internal parasites of spiders. The eggs are laid in large numbers on vegetation and hatch into tiny, flat-

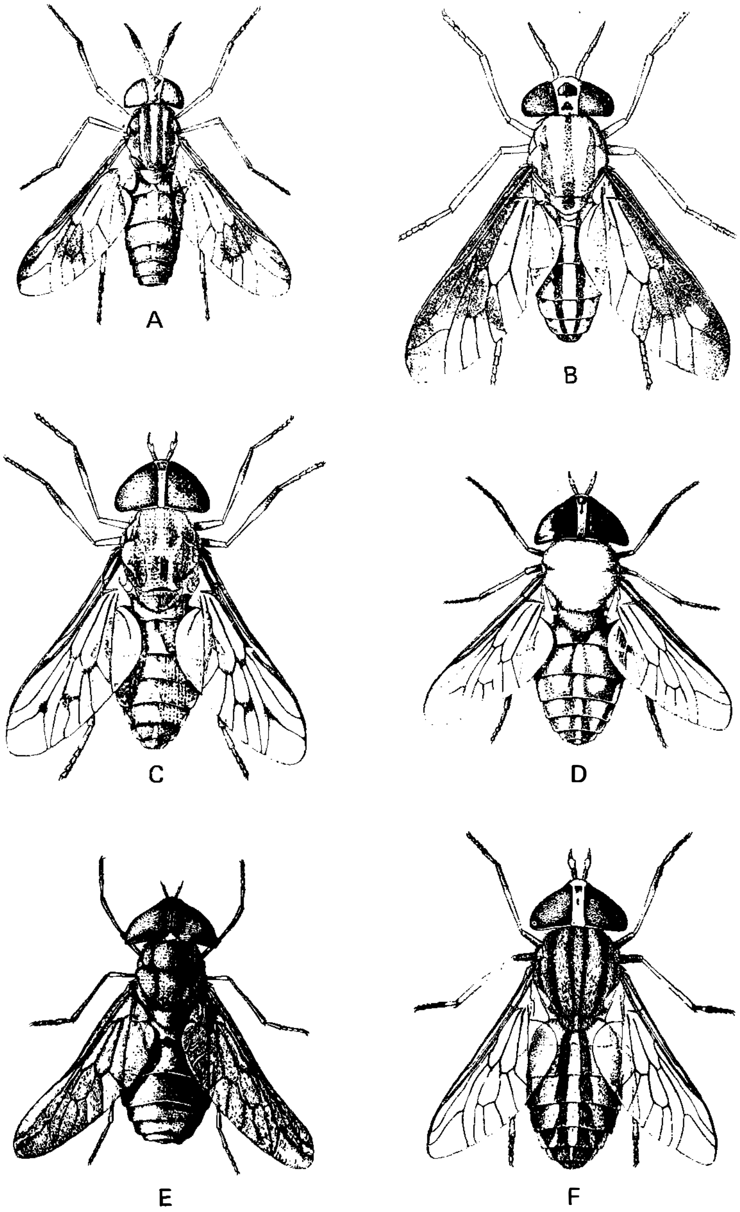

Figure 34–49 Horse and deer flies (Tabanidae). A, *Chrysops univittatus* Macquart; B, *Chrysops pikei* Whitney; C, *Tabanus sulcifrons* Macquart; D, *Tabanus quinquevittatus* Wiedemann; E, *Tabanus atratus* Fabricius; F, *Tabanus lineola* Fabricius. (Courtesy of Schwardt and Hall and the Arkansas Agricultural Experiment Station.)

tened larvae called *planidia*. The planidia eventually attach to and enter the body of a passing spider. Pupation occurs outside the host, often in the host's web.

Family **Nemestrinidae—Tangle-Veined Flies:** These are medium-sized, rather stout-bodied flies, with a somewhat aberrant wing venation (Figure 34–111). Some are hairy and beelike in appearance. They live in open fields of fairly high vegetation. They hover persistently, and are very fast fliers. Some species live on flowers. The group is a small one (6 North American species), and its members are relatively rare. Most species are western. The species whose larvae are known are parasites of other insects: species of *Trichopsidea* parasitize grasshoppers, and species of *Hirmoneura* attack scarabaeid beetle larvae. Nemestrinids are often important in controlling grasshopper populations.

Family **Apioceridae—Flower-Loving Flies:** These are relatively large, elongate flies that resemble some of the robber flies (for example, Figure 34–51B,C), but they do not have the top of the head hollowed out between the eyes, and they have a different wing venation (M_1 and the veins anterior to it ending in front of the wing

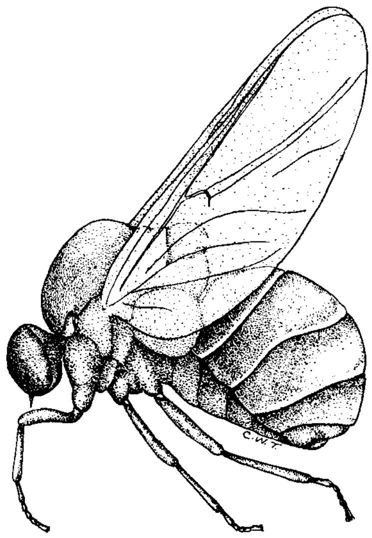

Figure 34–50 A small-headed fly, *Ogcodes* sp.

tip; see Figure 34–11J). This group is a small one (59 North American species), and its members are rather rare. They occur in the arid regions of the West, where they are often found on flowers.

Family **Asilidae—Robber Flies and Grass Flies:** This is a large group, with approximately a thousand North American species, many of which are quite common. The adults can found in a variety of habitats, but each species usually lives in a characteristic type. Adults are predaceous and attack a variety of insects, including wasps, bees, dragonflies, grasshoppers, and other flies. They often attack an insect as large as or larger than themselves. Most asilids capture their prey on the wing, but the grass flies (Leptogastrinae) usually attack resting insects. Some of the larger robber flies can inflict a painful bite if carelessly handled.

In robber flies, the top of the head is hollowed out between the eyes (Figure 34–51D), the face is more or less bearded, and they have a stout thorax with long, strong legs. Most are elongate, with a tapering abdomen (Figure 34–51B,C), but some are stout-bodied, very hairy, and resemble bumble bees or other Hymenoptera (Figure 34–51A). Still others are very slender, almost damselfly-like (Figure 34–52). The larvae live in soil, decaying wood, and similar places and feed chiefly on the larvae of other insects.

The family Asilidae is divided into four subfamilies, the Leptogastrinae, Laphriinae, Dasypogoninae, and Asilinae. The Leptogastrinae have been placed in a separate family by some authorities. They are very slender and elongate (Figure 34–52), and they generally live

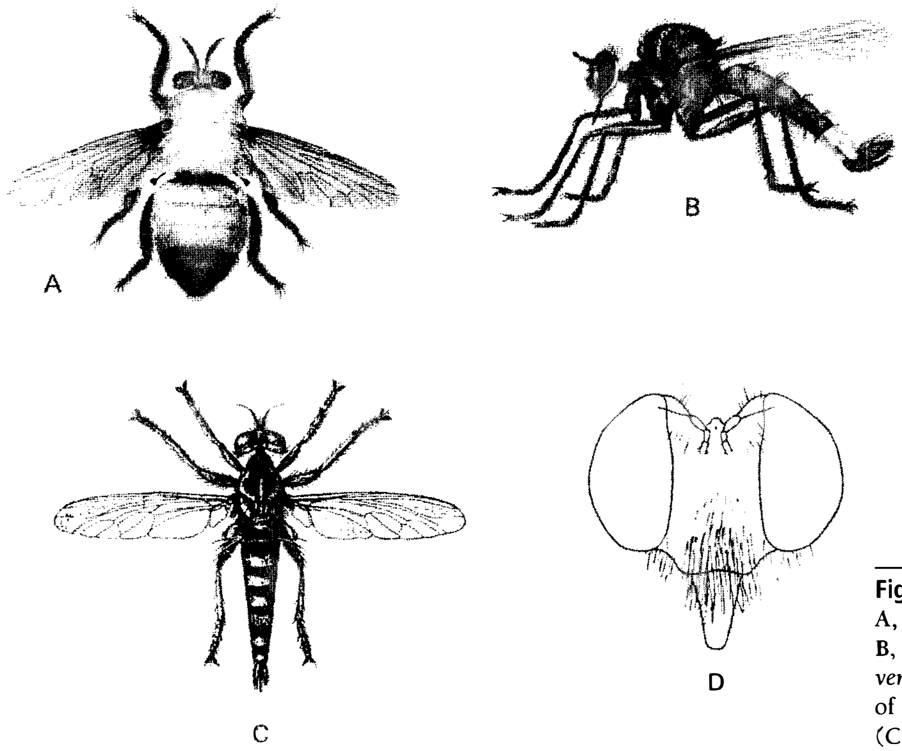

Figure 34–51 Robber flies. **A**, *Laphria lata* Macquart; **B**, *Efferia* sp.; **C**, *Promachus vertebratus* (Say); **D**, head of *Efferia*, anterior view. (C, courtesy of USDA.)

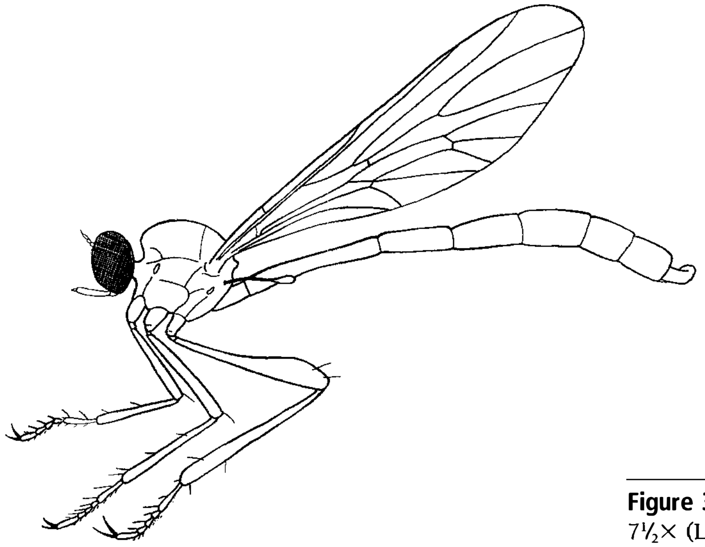

Figure 34–52 A grass fly, *Psilonyx annulatus* (Say). 7½× (Leptogastrinae, Asilidae).

in grassy areas, where they feed on small, soft-bodied, usually resting prey.

Family **Bombyliidae—Bee Flies:** This is a large group (about 900 known North American species), and its members are widely distributed. Bee flies are fairly common insects, probably more common in the arid areas of the Southwest than elsewhere. Most are stout-bodied, densely hairy flies of medium to large size. A few are slender and not very hairy, and some are very small (some Mythicomyiinae are only 1.2 mm long). Many have a long, slender proboscis.

The classification of bee flies is an area of active research and likely revision in the future. The Mythicomyiinae are recognized by some as a distinct family. Some authorities place one species in North America, *Apystomyia elinguis* Melander., from California, in its own family, the Apystomyiidae.

Bee flies are found on flowers or hovering over or resting on the ground or grass in open sunny places. They often visit water holes in arid regions. The wings at rest are usually held outstretched. Most species are very fast fliers, and when caught in an insect net, they buzz much like bees. Many have banded or spotted wings (Figure 34–53).

Bee fly larvae, as far as known, are either parasitic on the immature stages of other insects (Lepidoptera, Hymenoptera, Coleoptera, Diptera, and Neuroptera), or predaceous on grasshopper eggs.

Family **Hilarimorphidae:** The hilarimorphids are small (1.8 to 7.2 mm long), robust, dark-colored flies, with the wings hyaline to pale brown. There are 26 species, all in the genus *Hilarimorpha*, in North America. They are widely distributed, but rare. Adults have been collected on willows along narrow, gravel-bottomed streams. The immature stages are unknown.

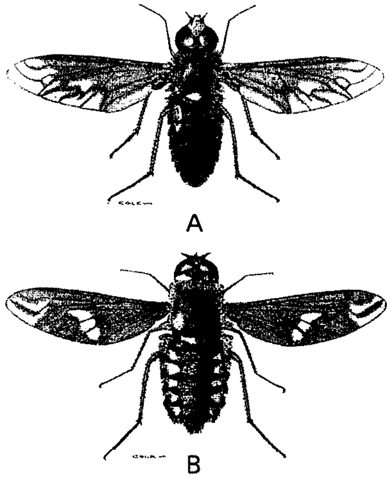

Figure 34–53 Bee flies. A, *Poecilanthrax alpha* (Osten Sacken); B, *P. signatipennis* (Cole). (Courtesy of Cole and the New York Entomological Society.)

Family **Mydidae—Mydas Flies:** The mydas flies are very large, elongate flies, with long, four-segmented antennae. *Mydas heros* (Perty), from Brazil and Colombia, is 54 mm long and is one of the largest dipterans known. There are 51 North American species in this family, and most are western. The species most likely to be encountered in the East is *Mydas clavatus* (Drury), which is black with the second abdominal segment yellow or orange (Figure 34–54). Little is known of the

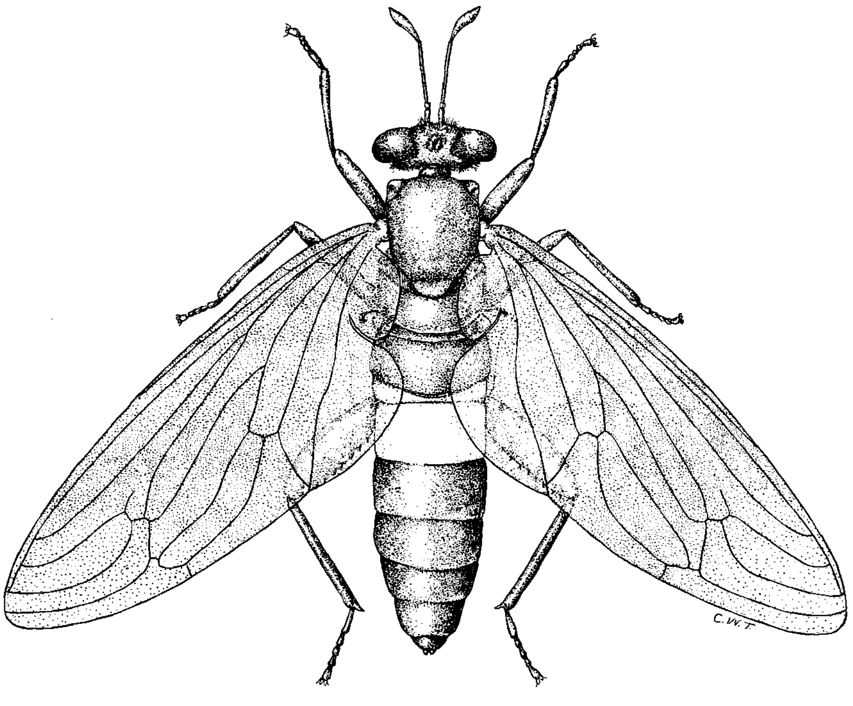

Figure 34–54 A mydas fly, *Mydas clavatus* (Drury).

habits of the mydas flies, but the larvae live in decaying wood and are predaceous. The adults are probably also predaceous.

***Family* Scenopinidae—Window Flies:** The window flies are rather uncommon flies of medium or small size and are usually blackish. The common name is derived from the fact that one species, *Scenopinus fenestralis* (L.) (Figure 34–55), is sometimes common on windows. The larva of this species is said to feed on the larvae of carpet beetles. The larvae of other species feed on decaying wood and fungi. This is a fair-sized group, with 139 North American species, most of which occur in the West.

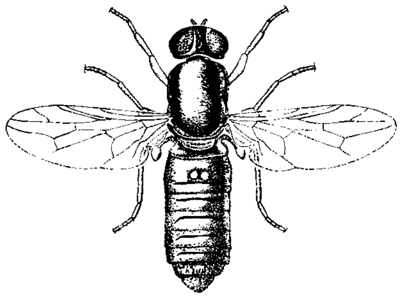

Figure 34–55 A window fly, *Scenopinus fenestralis* (L.). (Redrawn from USDA.)

***Family* Therevidae—Stiletto Flies:** These flies are of medium size, are usually somewhat hairy or bristly, and often have a pointed abdomen (Figure 34–56A,B). They are superficially similar to some robber flies, but the top of the head is not hollowed out between the eyes. This is a fair-sized group (about 141 North American species), but the adults are not common. They are most likely to be found in dry, open areas such as meadows and beaches. Little is known of the feeding habits of the adults, but they are probably plant feeders. The larvae are predaceous and usually live in sand or decaying wood.

***Family* Empididae—Dance Flies:** The dance flies are so named because the adults sometimes occur in swarms, flying with an up-and-down movement. This group is a large one (more than 760 North American species), and many species are fairly common. All are small, and some are minute (length 1.5 to 12.0 mm). Most are dark-colored, but none are metallic. Most have a large thorax and a long, tapering abdomen. The male genitalia are terminal and often are rather conspicuous (Figure 34–57).

Dance flies are found in a variety of situations, usually in moist places where there is an abundance of vegetation. They are predaceous on smaller insects (some are important predators of mosquitoes), but they often frequent flowers and feed on nectar.

Many species of dance flies have rather interesting mating habits. The males sometimes capture prey and

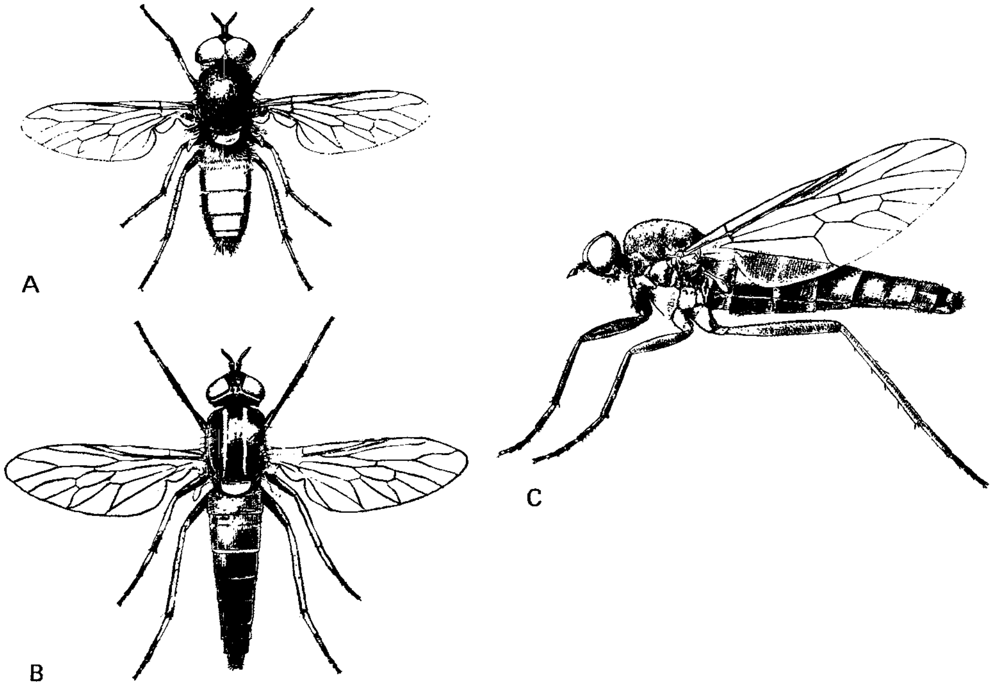

Figure 34–56 A, *Psilocephala aldrichi* Coquillet, female (Therevidae); B, same, male; C, *Caenotus inornatus* Cole, female (Bombyliidae). (Courtesy of Cole and the U.S. National Museum.)

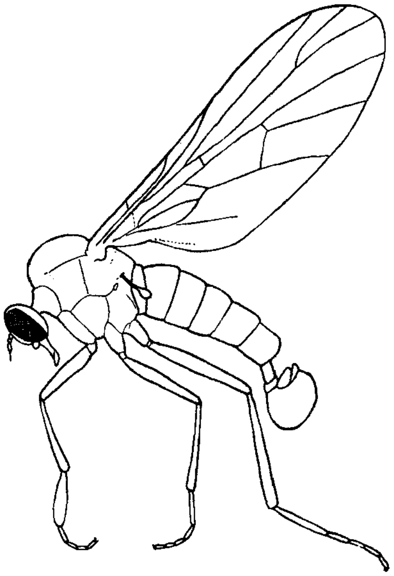

Figure 34–57 A dance fly (Empididae), 10×.

use it to attract females. Some species of *Hilara* and *Empis* that occur in the Northwest construct balloons, which they carry about as a means of attracting females. These balloons can be made of silk (spun from the basal segment of the front tarsi) or of a frothy material from the anus, and they usually contain prey.

Dance fly larvae live in a great variety of situations: In the soil, decaying vegetation, or dung, under bark, or in water. All are probably predaceous.

Family **Dolichopodidae—Long-Legged Flies:** The dolichopodids are small to minute flies that are usually metallic: greenish, bluish, or coppery. They are superficially similar to many of the muscoid flies (Schizophora) but lack a frontal suture and have a rather characteristic wing venation (Figure 34–14D–F): The r-m crossvein is very short or absent and is located in the basal fourth of the wing, and there is often a swelling of Rs where it forks. The male genitalia are usually large and conspicuous and folded forward under the abdomen (Figure 34–58). In the female the apex of the abdomen is pointed. The legs of the males are often peculiarly ornamented. Members of the genus *Melanderia*, which occur

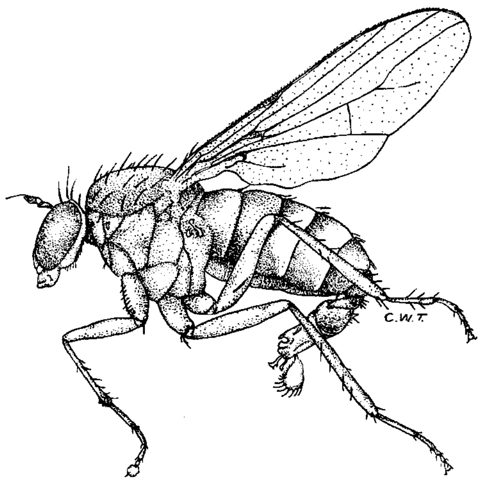

Figure 34–58 A long-legged fly, *Dolichopus pugil* Loew, male.

along the Pacific Coast, have the labellar lobes of the labium modified into mandible-like structures.

This group is a large one (more than 1,275 North American species), and its members are abundant in many places, particularly near swamps and streams, in woodlands, and in meadows. Many species live only in a particular type of habitat. The adults are predaceous on smaller insects. The adults of many species engage in rather unusual mating dances. The larvae live in water or mud, in decaying wood, in grass stems, and under bark. Not much is known of their feeding habits, but at least some are predaceous. The larvae of the genus *Medetera* live under bark and are predaceous on bark beetles (Coleoptera: Curculionidae, Scolytinae).

Family **Lonchopteridae—Spear-Winged Flies:** The members of this group are slender, yellowish or brownish flies less than 5 mm long, with wings somewhat pointed at the apex and with a characteristic venation (Figure 34–14H). They are usually fairly common in moist, shady, or grassy places. The larvae live in decaying vegetation. Males differ from females in venation: The M_3 cell is closed in the female (Figure 34–14H) and open in the male. Males are extremely rare, and these flies are probably parthenogenetic. This family contains only four North American species, in the genus *Lonchoptera*.

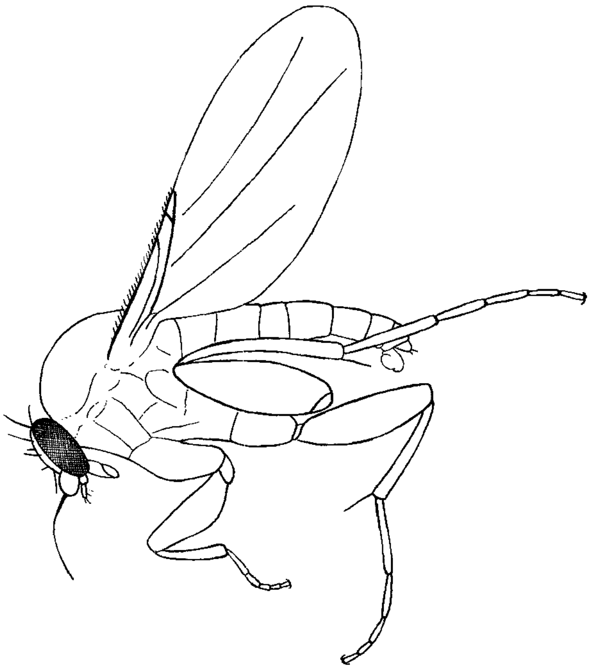

Figure 34–59 A humpbacked fly (Phoridae), 50×.

Family **Phoridae—Hump-Backed Flies:** The phorids are small or minute flies that are easily recognized by the humpbacked appearance (Figure 34–59), the characteristic venation (Figure 34–14G), the laterally flattened hind femora, and erratic manner in which they run. The adults are fairly common in many habitats but most abundant about decaying vegetation. The habits of the larvae are rather varied. Some live in decaying animal or vegetable matter; some live in fungi; some are internal parasites of various other insects; and some live as parasites or commensals in the nests of ants or termites. A few of the species that live in ant or termite nests (and some others as well) have reduced wings or lack them entirely. More than 370 species occur in North America.

Family **Pipunculidae—Big-Headed Flies:** The members of this group are small flies with the head very large and composed mostly of eyes (Figure 34–60). The wings are somewhat narrowed basally, and the anal cell is usually long and closed near the wing margin

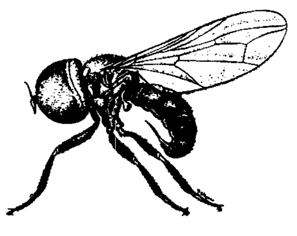

Figure 34–60 A big-headed fly, *Tomosvaryella subvirescens* (Loew), female. (Courtesy of Knowlton and the Utah Agricultural Experiment Station.)

(Figure 34–14J). The group is of moderate size (128 North American species), but its members are seldom common. The larvae are parasites of various hoppers, chiefly leafhoppers and planthoppers.

Family **Platypezidae—Flat-Footed Flies:** These flies are so named because of the peculiarly shaped hind tarsi, which are usually flattened or otherwise modified (Figure 34–26C). The tarsi are generally more flattened in females than in males. The flat-footed flies are small, usually black or brown, and live on low vegetation in damp woods. They often run about on leaves in an erratic, zigzag fashion. The males sometimes swarm in groups of up to 50 or more, the swarms dancing in the air a meter or so above the ground, with the hind legs hanging down. Females enter these swarms to select mates. If the swarm is disturbed, as by a swinging net, the flies scatter and reform the swarm again a little higher up (out of net reach). Adults of the genus *Microsania* are attracted to smoke, and are often called "smoke flies." The larvae of flat-footed flies live in fungi.

Family **Syrphidae—Hover Flies or Flower Flies:** This is a large group (about 870 North American species), and many species are very abundant. Syrphids can be found almost everywhere, but different species live in different types of habitats. The adults are often common about flowers and frequently do a great deal of hovering. Different species vary quite a bit in appearance (Figure 34–61), but (with a few exceptions) they can be recognized by the spurious vein in the wing between the radius and the media (Figure 34–15A–C, *spv*). Many are brightly colored and resemble various bees or wasps. Some look much like honey bees, others like bumble bees, and others like wasps, and the resemblance is often very striking. None of the syrphids bite or sting.

Syrphid larvae vary considerably in habits and appearance (Figure 34–62). Many are predaceous on aphids, others live in the nests of social insects (ants, termites, or bees), others live in decaying vegetation or rotting wood, others live in highly polluted aquatic habitats, and a few feed on growing plants. The larvae of *Eristalis* (Figure 34–62D,E), which live in highly polluted water, have a very long breathing tube and are commonly called "rattailed maggots." The adults of this genus (Figure 34–61D) resemble bees. Rattailed maggots are sometimes responsible for intestinal myiasis in humans.

Calyptratae *and* **Acalyptratae—Muscoid Flies or Schizophora:** The muscoid flies, with 56 families and nearly 7,000 known North American species, make up about one third of the order, and are to be found almost everywhere. They can be recognized by the presence of a frontal suture (Figure 34–5A, *fs*) on the lower part of the front of the head, arching up over the base of the antennae. Most are relatively stout-bodied, with somewhat reduced wing venation (Figures 34–22, 34–24) and characteristic bristles on the head and thorax (which provide taxonomic characters).

Many of the muscoid flies are small, and identifying them is often difficult. Moreover, the distinction

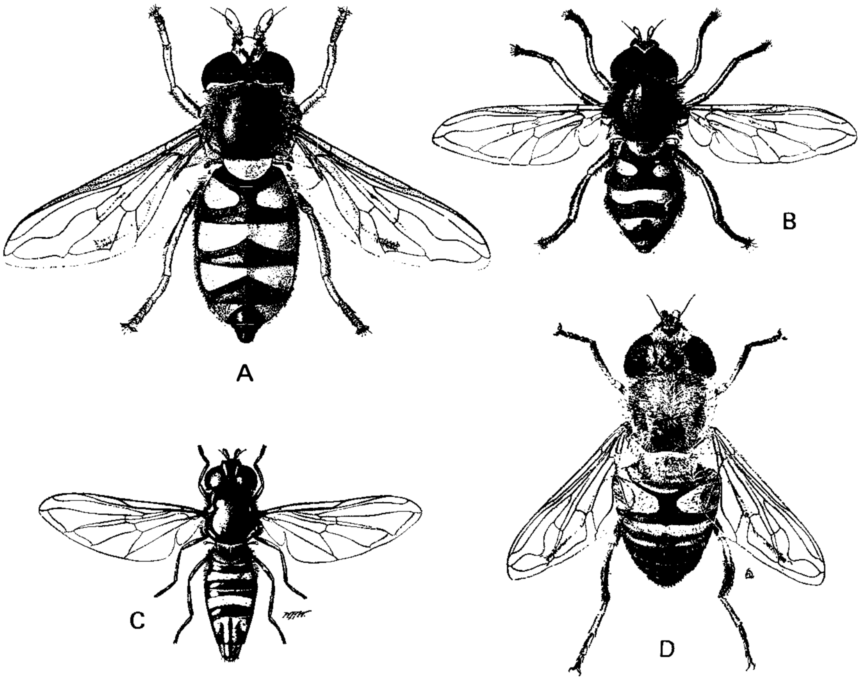

Figure 34–61 Syrphid flies. A, *Didea fasciata* Macquart; B, *Syrphus torvus* Osten Sacken; C, *Allograpta obliqua* (Say); D, *Eristalis tenax* (L.). (A, B, courtesy of Metcalf and the Maine Agricultural Experiment Station; C, D, courtesy of USDA.)

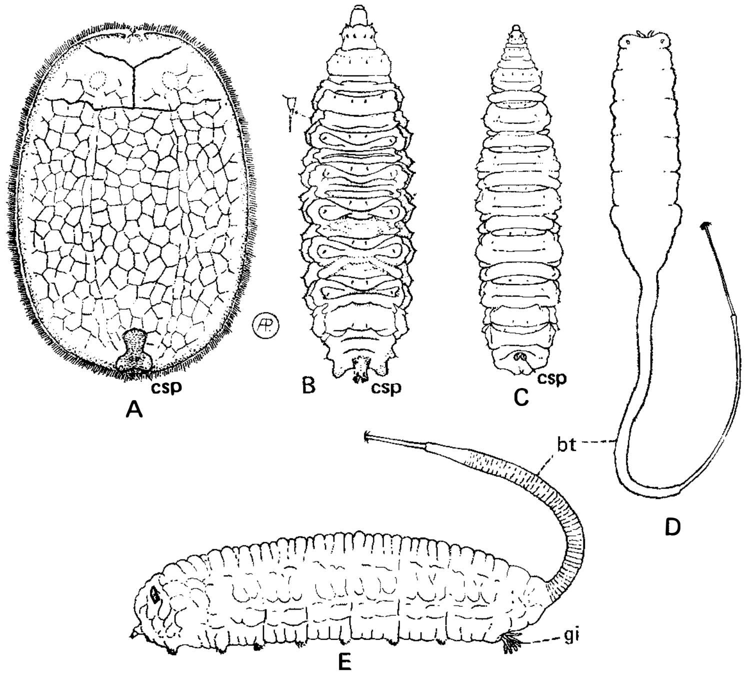

Figure 34–62 Larvae of syrphid flies. A, *Microdon* sp., 50×; B, *Pipiza femoralis* Loew, 50×; C, *Syrphus vittafrons* Shannon, $3\frac{1}{2}$×; D, E, *Eristalis* spp. (D, 2×; E, 3.5×). *bt*, breathing tube; *csp*, caudal spiracle; *gi*, gills. (Courtesy of Peterson; reprinted by permission.)

between families is often not very clear, and different authorities have placed many genera in different families. Some species (for example, the two species of *Latheticomyia*, here placed in the family Pseudopomyzidae) were originally described as being of uncertain family position.

The muscoids fall into two main groups, the Acalyptratae (45 families, Micropezidae through Ephydridae) and the Calyptratae (10 families, Anthomyiidae through Tachinidae). These names refer to the development of the calypteres, which are large and well developed in most calyptrates and very small in the acalyptrates. These two groups also differ (with a few exceptions) in the structure of the second antennal segment (Figure 34–19A,B) and the sutures on the dorsal side of the thorax (Figure 34–19C,D) (see key, couplet 66). Each of these groups contains more than 3,400 North American species.

Calyptratae—Calyptrate Muscoid Flies: These flies live nearly everywhere, often in large numbers. Some of the calyptrate groups are fairly distinct and easily recognized, but others are not, and there are differences of opinion about the taxonomic placement of some.

For purposes of identification, the families in this section can be divided into four groups:

1. Flat and leathery, with the coxae separated, and winged or wingless; ectoparasites of birds and mammals: Hippoboscidae
2. Robust, hairy, beelike, with the mouthparts reduced (bot and warble flies): Oestridae
3. Somewhat similar to a house fly in general appearance, usually with no hypopleural or pteropleural bristles, and the R_5 cell usually parallel-sided: Scathophagidae, Anthomyiidae, Fanniidae, and Muscidae
4. Similar to group 3, but with hypopleural and pteropleural bristles, and the R_5 cell narrowed or closed distally: Calliphoridae, Sarcophagidae, Rhinophoridae, and Tachinidae

***Family* Anthomyiidae:** This is a large group (more than 600 North American species), and most are blackish and about the size of a house fly or smaller. They differ from the Muscidae in having the anal vein (Cu_2+2A) reaching the wing margin, at least as a fold. Most Anthomyiidae have fine hairs on the underside of the scutellum (Figure 34–17D). Those Anthomyiidae that lack these hairs (Fucelliinae) have cruciate frontal bristles and usually four sternopleural bristles, and they have the costa spinose. Most of the Anthomyiidae are plant feeders in the larval stage, and many of these feed on the roots of the host plant; some (Figure 34–63) are serious pests of garden or field crops. The larvae of the Fucelliinae, a small group occurring chiefly in the West and in Canada, are aquatic and predaceous.

***Family* Calliphoridae—Blow Flies:** Blow flies are to be found practically everywhere, and many species are of considerable economic importance. Most blow flies are about the size of a house fly or a little larger, and many are metallic blue or green (Figure 34–64). Blow

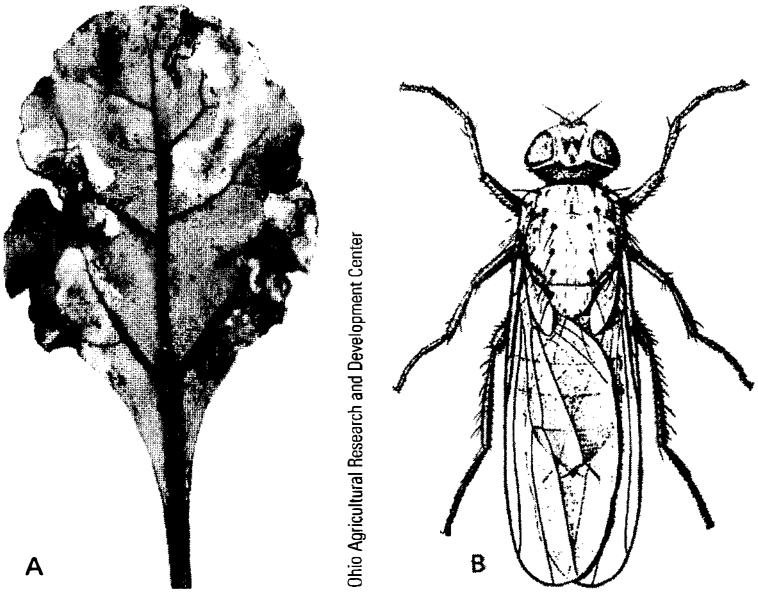

Figure 34–63 A, mines of the spinach leafminer, *Pegomya hyoscyami* (Panzer) (Anthomyiidae); B, adult female of the seedcorn maggot, *Hylemya platura* (Meigen) (Anthomyiidae), 8×. (A, courtesy of the Ohio Agricultural Research and Development Center; B, courtesy of USDA.)

flies are very similar to flesh flies (Sarcophagidae), and some authorities put the two groups in a single family, the Metopiidae. Blow flies are often metallic in color and have the arista of the antennae plumose at the tip, whereas flesh flies are blackish with gray thoracic stripes (Figure 34–65A) and have the arista bare or only the basal half plumose. Blow flies usually have two (rarely three) notopleural bristles, and flesh flies usually have four (Figure 34–20).

Most blow flies are scavengers, the larvae living in carrion, excrement, and similar materials. The most common species are those that breed in carrion. These species lay their eggs on bodies of dead animals, and the larvae feed on the decaying tissues of the animal. To most people a dead animal teeming with maggots (mostly the larvae of blow flies) is a nauseating thing, but these insects are performing a valuable service in helping to remove dead animals from the landscape. The larvae of some of the species that breed in carrion, particularly *Phaenicia sericata* (Meigen) and *Phormia regina* (Meigen), when reared under aseptic conditions, have been used in treating such diseases as osteomyelitis in humans. However, many of these flies may act as mechanical vectors of various diseases. Dysentery frequently accompanies high blow-fly populations.

Figure 34–64 A blow fly, *Lucilia illustris* (Meigen).

Flies in this family are the "house flies" of the western United States, especially the Southwest. They are far more common than *Musca* in houses in that part of the country.

Some blow flies lay their eggs in open sores of animals or people. In some cases the larvae feed only on decaying or suppurating tissue, but in other cases they can attack living tissue. The screwworm fly, *Cochliomyia hominivorax* (Coquerel) (Figure 34–65B), is a species in the latter category. It lays its eggs in wounds or in the nostrils of its host, and its larvae can cause considerable damage. In recent years the number of screwworm flies in the South and Southwest has been greatly reduced by releasing large numbers of sterile male flies. The females mate only once, and if a female mates with a sterile male, its eggs fail to hatch.

When fly larvae become parasitic on humans or animals, the condition is spoken of as *myiasis*. Flies such as the screwworm can develop in surface wounds and cause cutaneous myiasis or in the nasal cavities and cause nasal myiasis. A few other flies in this group have been known to develop in the human intestine and cause intestinal myiasis. Myiasis in humans is relatively

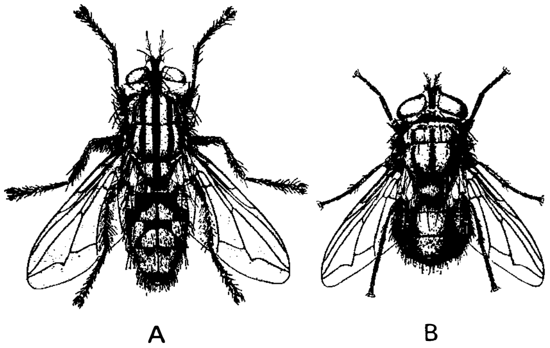

Figure 34–65 A, a flesh fly, *Sarcophaga haemorrhoidalis* (Fallén); B, the screwworm fly, *Cochliomyia hominivorax* (Coquerel) (Calliphoridae). (Courtesy of USDA.)

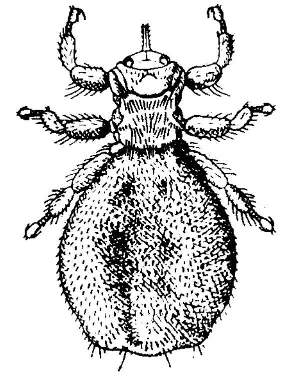

Figure 34–66 The sheep ked, or sheep-tick, *Melophagus ovinus* (L.). (Courtesy of Knowlton, Madsen, and the Utah Agricultural Experiment Station.)

rare in the United States and Canada, and it is probably more or less accidental. In the South and Southwest, it has been very important in domestic animals.

***Family* Fanniidae:** This is a small family of four genera and 112 species, most in the genus *Fannia*. Most of its species differ from muscids in having 3A curved outward distally, so that Cu_2+2A if extended would meet it (Figure 34–18D). This group is sometimes considered a subfamily of Muscidae. These flies look very much like small house flies, and in some areas are a more important household pest than *Musca domestica* L. The larvae breed in excrement and various types of decaying materials.

***Family* Hippoboscidae—Louse Flies and Bat Flies:** This group includes both winged and wingless forms. Most of the winged forms are dark brownish and somewhat smaller than house flies. They are most likely to be found on birds. These flies are easily recognized by their flat shape and leathery appearance. They are the only flies likely to be found on living birds. The sheep ked, *Melophagus ovinus* (L.) (Figure 34–66), is a fairly common wingless louse fly. It is about 6 mm long and reddish brown, and the adult is a parasite of sheep.

The bat flies are ectoparasites of bats. They can be winged, wingless, or can have the wings reduced in size. Some species have no ocelli, and the compound eyes are small or absent. The five species in the genus *Basilia* are small, wingless, and spiderlike with the head folded back into a groove on the dorsum of the thorax. The compound eyes are small and two-faceted. Only 11 species of bat flies occur in North America, and they are very seldom encountered. They occur in the South and West.

***Family* Muscidae:** This is a large group (620 known North American species), and its members are almost everywhere. Many are important pests. The Muscidae differ from the Anthomyiidae in having the anal vein (Cu_2 +2A) short and not reaching the wing margin, and some have the R_5 cell narrowed apically. The house fly, *Musca domestica* L., breeds in filth of all kinds and is often very abundant. It is a vector of typhoid fever, dysentery, yaws, anthrax, and some forms of conjunctivitis. It does not bite. The face fly, *Musca autumnalis* DeGeer, is an important pest of cattle. It gets its name from its habit of clustering on the face of cattle (Figure 34–67). The stable fly and horn fly are biting flies; but unlike mos-

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Figure 34–67 Face flies, *Musca autumnalis* DeGeer, on a cow.

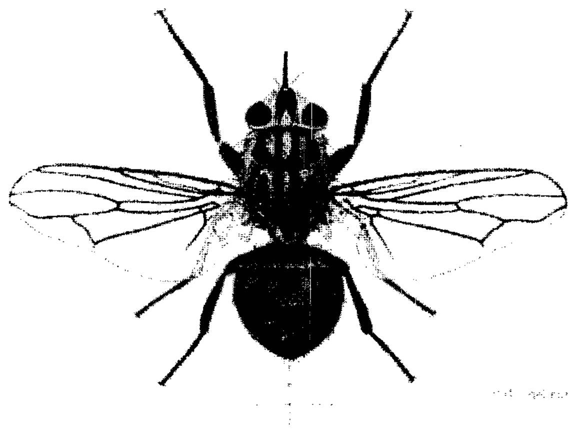

Illinois Natural History Survey

Figure 34–68 The stable fly, *Stomoxys calcitrans* (L.).

Figure 34–69 Two common muscids, showing the difference in the shape of the proboscis. Left, stable fly; right, house fly. (Courtesy of the Illinois Natural History Survey.)

quitoes, horse flies, and others, both sexes bite. The stable fly, *Stomoxys calcitrans* (L.) (Figure 34–68), is very similar to the house fly in appearance (Figure 34–69). It breeds chiefly in piles of decaying straw. The horn fly, *Haematobia irritans* (L.), which is similar to the house fly in appearance but smaller, is a serious pest of cattle that breeds in fresh cow dung.

Family **Oestridae—Bot Flies and Warble Flies:** The members of this group are robust, hairy, and somewhat beelike. The mouth opening is small, and the mouthparts are vestigial or lacking (Figure 34–17A). The larvae are endoparasites of mammals, and some are important pests of livestock.

The 41 North American species in this family are arranged in six genera: *Cuterebra* (26 species), *Gasterophilus* (4 species), *Hypoderma* (3 species), *Oestrus* (1 species), *Cephenemyia* (6 species), and *Suioestrus* (1 species).

Gasterophilus differs from the other oestrids in having M_{1+2} straight and reaching the wing margin behind the apex of the wing, and m is about opposite r-m (Figure 34–18E). In the other oestrids M_{1+2} bends forward apically and ends either in R_{4+5} (*Oestrus*, Figure 34–18F) or in the wing margin in front of the wing tip (*Cuterebra*, *Hypoderma*, and *Cephenemyia*), and m is well distad of r-m. Species of *Cuterebra* have a strongly projecting scutellum, and the postscutellum is not developed (Figure 34–13C), whereas *Hypoderma*, *Oestrus*, and *Cephenemyia* have a scutellum that is quite short, and the postscutellum is usually well developed (Figure 34–17B). In *Hypoderma* the apical portion of M_{1+2} (the part beyond m) extends almost straight to the wing margin (Figure 34–70B), whereas in *Cephenemyia* the apical portion of M_{1+2} continues in the same direction a short distance beyond m, then bends forward at a right angle and extends to the wing margin (much as in Figure 34–18A).

Gasterophilus, the horse bot flies, are very similar to honey bees in appearance (Figure 34–70A). The larvae infest the alimentary tract of horses and are often serious pests. Three species occur commonly in the United States, *Gasterophilus intestinalis* (DeGeer), *G. nasalis* (L.), and *G. haemorrhoidalis* (L.). A fourth species, *G. inermis* (Brauer), is very rare. In *G. intestinalis* the eggs are laid on the legs or shoulders of the horse and are taken into the mouth when the animal licks these parts. In *G. nasalis* the eggs are usually laid on the underside of the jaw, and the larvae are believed to make their way through the skin into the mouth. In *G. haemorrhoidalis* the eggs are laid on the lips of the horse. The larvae develop in the stomach (*intestinalis*), duodenum (*nasalis*), or rectum (*haemorrhoidalis*). When ready to pupate, they pass out of the alimentary tract in the feces and pupate in the ground.

Species of *Cuterebra*, the robust bot flies, are large, stout-bodied, rather hairy flies that resemble bees. The larvae are parasites of rabbits and rodents. One tropical species in this subfamily, *Dermatobia hominis* (L.) (Figure 34–70D), attacks livestock and occasionally people. This species lays its eggs on mosquitoes (principally mosquitoes in the genus *Psorophora*). The eggs hatch, and the larvae penetrate the skin when the mosquito feeds on livestock or humans. Stable flies and other muscids may also serve as carriers of *D. hominis* eggs to humans.

The ox warble flies, *Hypoderma bovis* (L.) and *H. lineatum* (de Villers), are serious pests of cattle. A third species of *Hypoderma* is a parasite of caribou. The eggs of these flies are usually laid on the legs of cattle, and the larvae penetrate the skin and migrate, often by way of the esophagus, to the back, where they develop in swellings or "warbles" just under the skin. When full grown, they escape through the skin and pupate in the ground. Adult ox warble flies are very fast fliers, and although they do not bite or injure the cattle when they oviposit, they are very annoying to cattle. Ox warble can seriously affect the health of cattle, and the

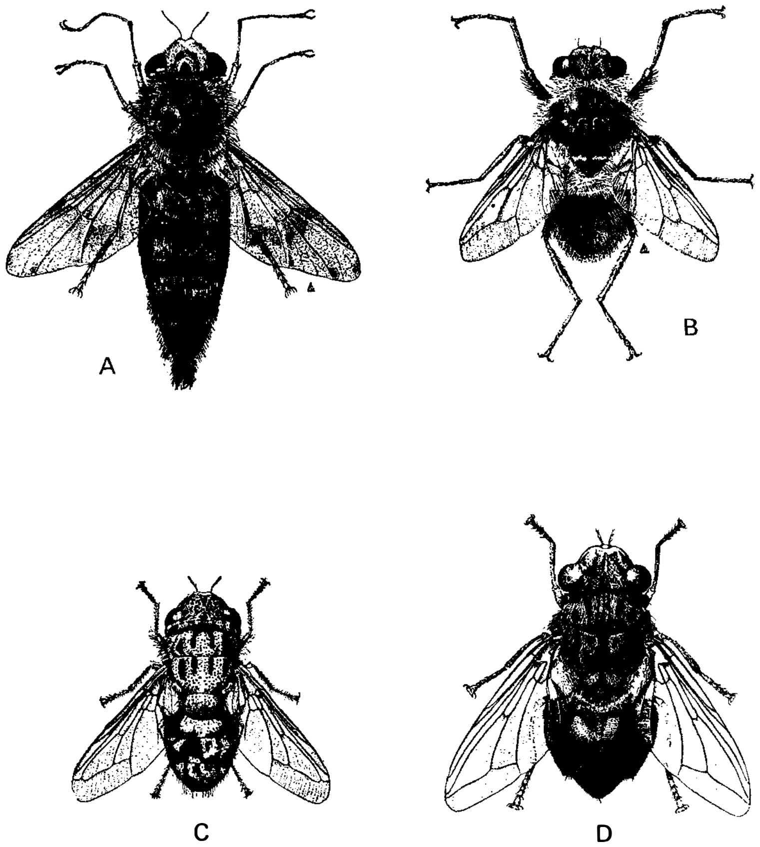


Figure 34–70 Bot and warble flies (Oestridae). A, a horse bot fly, *Gasterophilus intestinalis* (DeGeer), female; B, ox warble fly, *Hypoderma lineatum* (de Villers), female; C, sheep bot fly, *Oestrus ovis* L., female; D, human bot fly or torsalo, *Dermatobia hominis* (L., Jr.), female. (Courtesy of USDA.)

holes made in the skin by the escaping larvae reduce the value of the hide when it is made into leather.

The only Nearctic species of *Oestrus* is the sheep bot fly, *Oestrus ovis* L. (Figure 34–70C). The sheep bot fly is viviparous and deposits its larvae in the nostrils of sheep (rarely, also in humans). The larvae feed in the frontal sinuses of the sheep. The genus *Cephenemyia* includes six species that are parasites of cervids (deer, moose, elk, and so forth). Finally, *Suioestrus cookii* Townsend is a parasite of pigs.

***Family* Rhinophoridae:** These flies are similar to the tachinids (with which they were formerly classified) but differ in having a weakly developed postscutellum and narrow calypteres. The eyes are sometimes hairy. The group is a small one, with only four North American species. *Melanophora roralis* (L.), which occurs in the East, is probably the most common species. It is a parasite of isopods.

***Family* Sarcophagidae—Flesh Flies:** Flesh flies are very similar to some blow flies, but are generally blackish with gray thoracic stripes (never metallic) (Figure 34–65A). The adults are common insects and feed on various sugar-containing materials such as nectar, sap, fruit juices, and honeydew. The larvae vary considerably in habits, but nearly all feed on some sort of animal material. Many are scavengers, feeding on dead animals. Some are parasites of other insects (especially various beetles and grasshoppers). A few are parasites of vertebrates, usually developing in skin pustules, and some of these occasionally infest humans. Many species (most of the Miltogramminae) lay their eggs in the nests of various bees and wasps, where their larvae feed on the materials with which these nests are provisioned.

***Family* Scathophagidae—Dung Flies:** The members of this group are very similar to the Anthomyiidae (the family in which they are sometimes placed), but differ in having no fine hairs on the underside of the scutellum, usually just one sternopleural bristle, and no cruciate frontal bristles.

Probably the most common members of the Scathophagidae are yellowish and quite hairy (see Figure 4–5), and their larvae live in dung. Other species are dark-colored, and the larvae live in a variety of situations: Some are plant feeders (a few of these are leaf miners), some feed in rotting seaweeds, and some are aquatic. The Scathophagidae are a large group (149 North American species) and contain many common species.

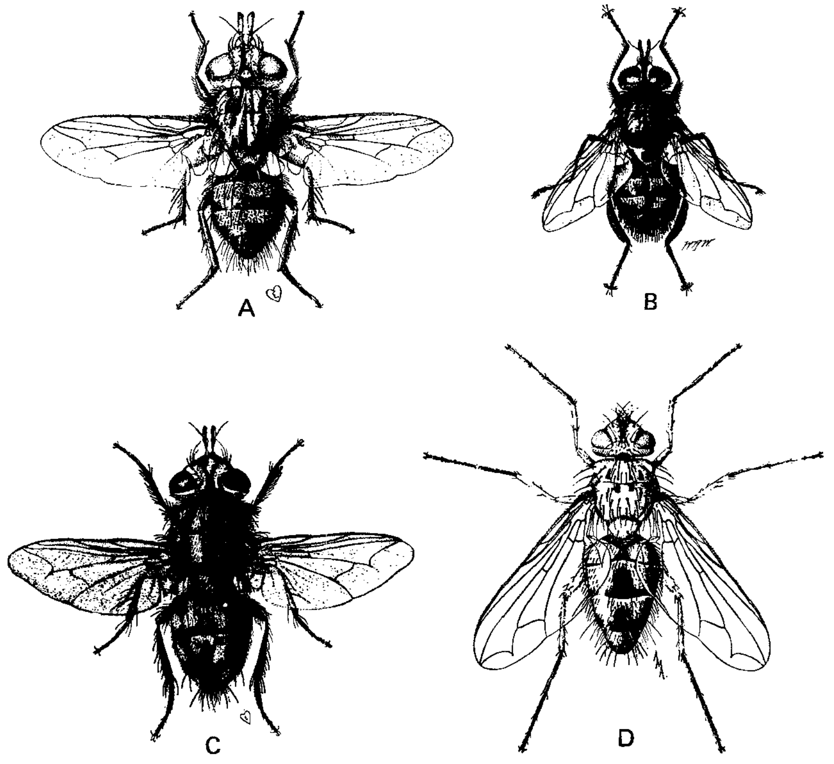


Figure 34–71 Tachinid flies. A, *Euphorocera claripennis* (Macquart); **B**, *Winthemia quadripustulata* (Fabricius); C, *Archytas marmoratus* (Townsend); **D**, *Dexilla ventralis* (Aldrich). (Courtesy of USDA.)

Family **Tachinidae:** This family is the second largest in the order (at least in North America), with about 1,350 known North American species, and its members are to be found almost everywhere. It is a group very valuable to humans, because the larval stages are parasites of other insects, and many species aid in keeping pest species in check.

Tachinids are usually relatively easy to recognize. Both the hypopleural and the pteropleural bristles are developed, and the postscutellum is prominent (Figure 34–13B). The terga usually overlap the ventral sclerites of the abdomen, and the abdomen generally has a number of very large bristles in addition to the smaller ones. The first posterior (R_5) cell is narrowed or closed distally, and most species have the arista bare. Many tachinids are very similar in general appearance to muscids and flesh flies (Figures 34–71, 34–72A). Many are large, bristly, and beelike or wasplike in appearance.

Tachinids attack many different groups of insects, and although most tachinids are more or less restricted to particular hosts, a few can develop in a wide variety of hosts. Most tachinids attack the larvae of Lepidoptera, sawflies, or beetles, but some attack Hemiptera, Orthoptera, and some other orders, and a few attack other arthropods. A number of tachinids have been imported into the United States to help control introduced pests.

Most tachinids deposit their eggs directly on the body of their host, and it is not at all uncommon to find caterpillars with several tachinid eggs on them. On hatching, the tachinid larva usually burrows into its host and feeds internally (Figure 34–72B). When fully developed, it leaves the host and pupates nearby. Some tachinids lay their eggs on foliage. These eggs usually hatch into peculiar flattened larvae called ***planidia***, which remain on the foliage until they can attach to a suitable host when it passes by. In other species that lay their eggs on foliage, the eggs hatch when they are ingested (along with the foliage) by a caterpillar. The tachinid larvae then proceed to feed on the internal organs of the caterpillar. An insect attacked by tachinids is practically always killed eventually.

Acalyptratae—Acalyptrate Muscoid Flies: This is a large and diverse group (3,500 species). Many are small in body size and traditionally pose a challenge to the student for identification. The monophyly of Acalyptratae is not well established, and it may well represent a paraphyletic group.

Family **Micropezidae—Stilt-Legged Flies:** The members of this group are small to medium-sized elongate flies with very long legs. The first posterior (R_5) cell is narrowed apically, and the anal cell is often long and pointed (Figure 34–22C). The adults are found near moist places. Only 33 species occur in North America,

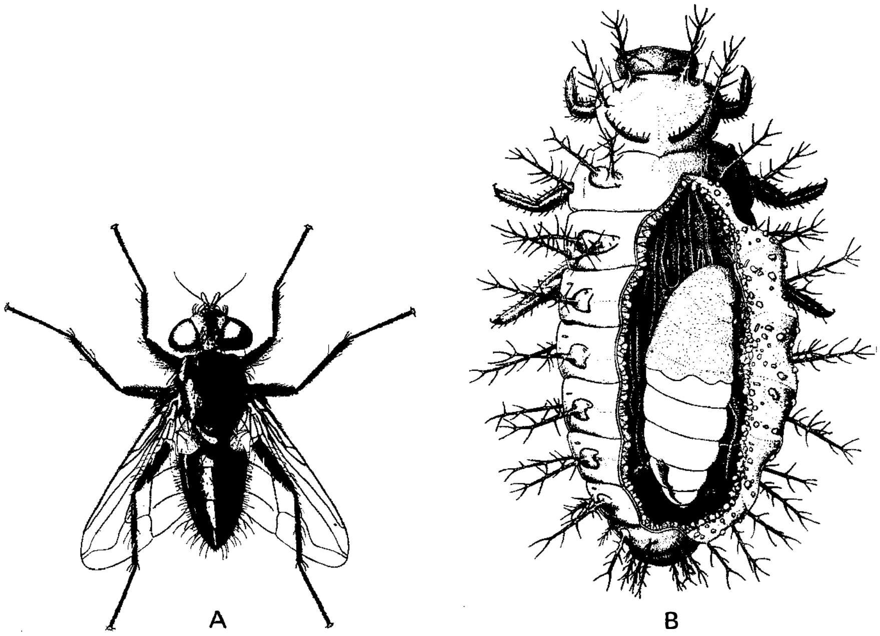


Figure 34–72 The bean beetle tachinid, *Aplomyiopsis epilachnae* (Aldrich). A, adult; B, a bean beetle larva dissected to show a larva of this tachinid inside it. (Courtesy of USDA.)

but the group is abundant in the tropics, where the larvae live in excrement.

Family **Neriidae—Cactus Flies**: This group is represented in the United States by two species occurring in the Southwest. The most common species, *Odontoloxozus longicornis* (Coquillett), ranges from southern Texas to southern California. It is slender, medium-sized, and grayish with brown markings, and it has long, slender legs and long, porrect antennae (Figure 34–23I). The larvae breed in decaying cacti, and the adults are usually found only on such cacti.

Family **Pseudopomyzidae**: The flies in this group that occur in the United States, *Latheticomyia tricolor* Wheeler and *L. lineata* Wheeler, are 2.5 to 3.5 mm long and black with yellow areas on the head, thorax, and legs. The front coxae are long and slender, nearly as long as the tibiae. The front femora have a few strong bristles ventrally in the distal half, and the hind femora have a single bristle at about three fourths their length. The wings are hyaline, the anal cell is well developed, 2A does not reach the wing margin, and the second basal and discal cells are confluent. They have been taken during late twilight, at banana-baited traps, in Arizona and Utah.

Family **Diopsidae—Stalk-Eyed Flies**: This group is largely tropical, and only two species, *Sphyracephala brevicornis* (Say) and *S. subbifasciata* Fitch, occur in North America. Most of the tropical species have the eyes situated at the ends of long stalks, but North American species have relatively short eyestalks (Figure 34–23J). Adults are blackish and about 4.5 mm long, with the front femora distinctly swollen. This species has been reared in the laboratory (from eggs laid by overwintered adults), but little is known of its life history in the field. The larvae feed on wet organic matter and probably live in sphagnum bogs. Adults are usually found in or near such habitats, often on skunk cabbage.

Family **Psilidae—Rust Flies**: The psilids are small to medium-sized flies, usually rather slender, with long antennae. They have a peculiar ridge or weakening across the basal third of the wing. In the genus *Loxocera,* the third antennal segment is very long and slender (Figure 34–21). The larvae live in the roots or galls of plants, and one species, *Psila rosae* (Fabricius), the carrot rust fly, often does considerable damage to carrots, celery, and related plants.

Family **Tanypezidae**: The Tanypezidae are medium-sized flies with rather long and slender legs. They live in moist woods and are quite rare. Only three species occur in the United States (in the Northeast), and nothing is known of their immature stages.

Family **Conopidae—Thick-Headed Flies**: The conopids are medium-sized, brownish flies, many of which super-

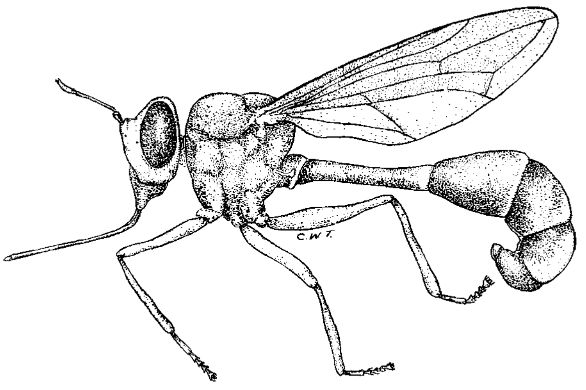


Figure 34–73 A thick-headed fly, *Physocephala furcillata* (Williston).

ficially resemble small thread-waisted wasps (Figure 34–73). The abdomen is usually elongate and slender basally, the head is slightly broader than the thorax, and the antennae are long. All species have a very long and slender proboscis. In some species the proboscis is elbowed. The wing venation (Figure 34–15D) is similar to that in the Syrphidae (Figure 34–15A–C), but there is no spurious vein. Conopids can be distinguished from syrphids lacking a spurious vein by their long, slender proboscis. In one genus (*Stylogaster*), the abdomen is slender and, in the female, terminates in a very long ovipositor that is as long as the rest of the body. The adults are usually found on flowers. The larvae are endoparasites, chiefly of adult bumble bees and wasps, and the flies usually oviposit on their hosts during flight.

Family **Lonchaeidae:** The lonchaeids are small, shining, blackish flies, with the abdomen in dorsal view oval and somewhat pointed apically. They live chiefly in moist or shady places. The larvae are mostly secondary invaders of diseased or injured plant tissues. A few feed on pine cones, fruits, or vegetables. The group contains about 120 North American species, and the adults are not very common.

Family **Pallopteridae—Flutter Flies:** The nine North American species in this group are rare and poorly known. They are medium-sized flies that usually have pictured wings and live in moist, shady places. The larvae of North American species are unknown, but the larvae of European species are plant feeders in flower buds and stems or live under the bark of fallen trees, where they prey on wood-boring beetle larvae.

Family **Piophilidae—Skipper Flies:** The skipper flies are usually less than 5 mm long and are rather metallic black or bluish (Figure 34–74A). The larvae are mostly scavengers, and some live in cheese and preserved meats. The larvae of the cheese skipper, *Piophila casei* (L.), are often serious pests in cheese and meats. The name "skipper" refers to the fact that the larvae can jump. This family includes *Actenoptera hilarella* (Zetterstedt), formerly placed in the family Neottiophilidae. This European species has been widely reported from Canada and the state of Washington.

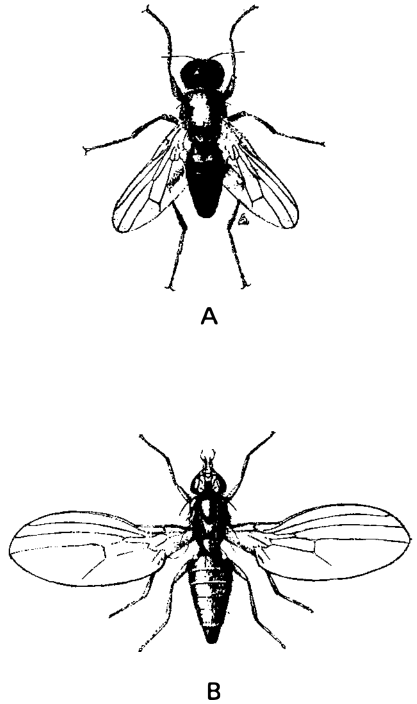


Figure 34–74 A, adult of the cheese skipper, *Piophila casei* (L.) (Piophilidae); B, a leaf-miner fly, *Cerodontha dorsalis* (Loew) (Agromyzidae). (Courtesy of USDA.)

Family **Pyrgotidae:** The pyrgotids are rather elongate flies of medium to large size, and they often have considerable coloring in the wings. The head is prominent and rounded, and there are no ocelli (Figure 34–75). This is a small group (nine North American species),

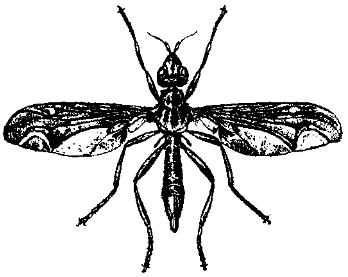


Figure 34–75 *Pyrgota undata* Wiedemann (Pyrgotidae). (Courtesy of USDA.)

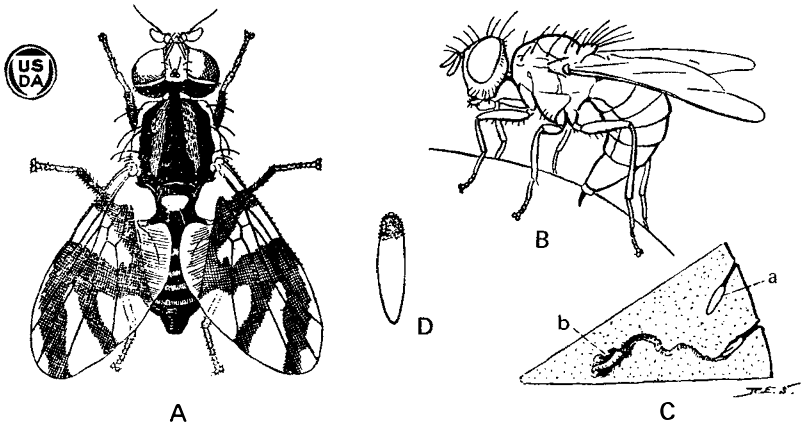


Figure 34–76 The apple maggot, *Rhagoletis pomonella* (Walsh) (Tephritidae). A, adult female, 7×; B, female puncturing skin of apple preparatory to depositing an egg; C, section of an apple showing an egg inserted at *a*, and a young maggot tunneling into the pulp at *b*; D, an egg (greatly enlarged). (Courtesy of USDA.)

and its members are not very common. The adults are mostly nocturnal and are often attracted to lights, and the larvae are parasites of adult june beetles.

Family **Richardiidae:** This is a small group (10 North American species) of uncommon to rare flies about which little is known. Most species have been taken at fruit-baited traps, and one species of *Omomyia* has been taken on yucca. In *Omomyia* the costa is spinose and the males are very hairy. These flies are known from Arizona and New Mexico. Most species in this family have patterned wings.

Family **Tephritidae—Fruit Flies:** The members of this group are small to medium-sized flies that usually have spotted or banded wings, the spotting often forming complicated and attractive patterns (Figures 34–76, 34–77). They can be recognized by the structure of the subcosta, which apically bends forward at almost a right angle and then fades out. In most species the anal cell has an acute distal projection posteriorly (Figure 34–24B). The adults are found on flowers or vegetation. Some species have the habit of slowly moving their wings up and down while resting on vegetation and are often called "peacock flies."

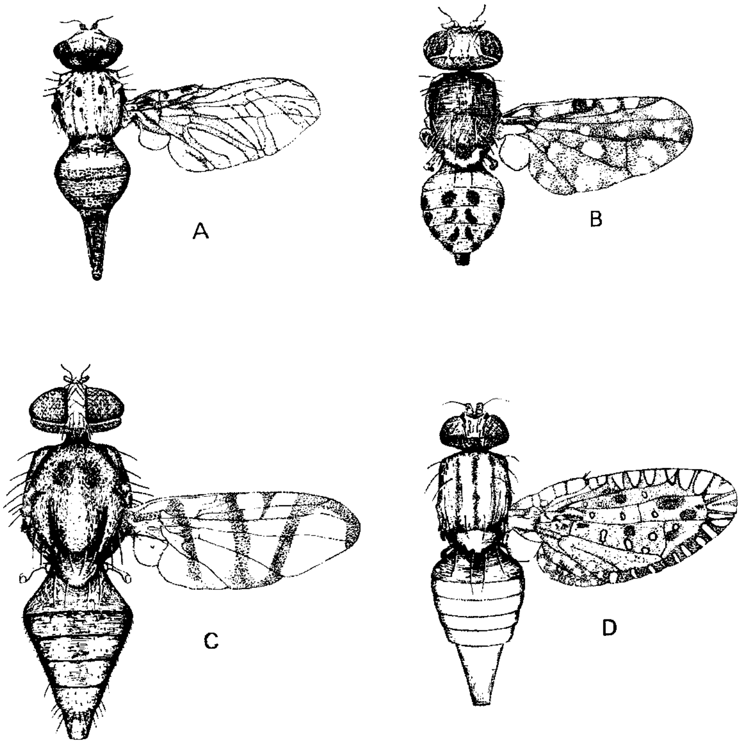
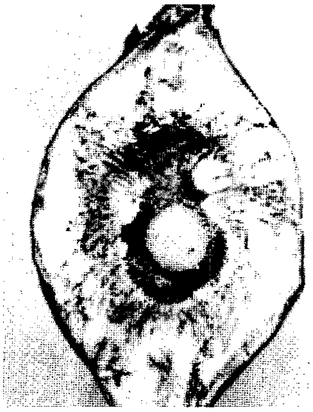


Figure 34–77 Fruit flies (Tephritidae). A, *Peronyma sarcinata* (Loew); B, *Acidogona melanura* (Loew); C, *Zonosemata electa* (Say); D, *Paracantha culta* (Wiedemann). (Courtesy of USDA.)



Illinois Natural History Survey

Figure 34–78 Gall of goldenrod gall fly, *Eurosta* sp. (Tephritidae), cut open to show the larva. (Courtesy of the Illinois Natural History Survey.)

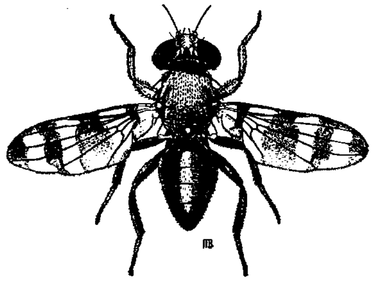


Figure 34–79 A picture-winged fly, *Euxesta stigmatis* Hendel, 6× (Ulidiidae). (Courtesy of Wolcott and the Journal of Agriculture of the University of Puerto Rico.)

This group is a large one (300 North American species), and many species are quite common.

The larvae of most tephritids feed on plants, and some are rather serious pests. The larva of *Rhagoletis pomonella* (Walsh), usually called the "apple maggot," tunnels in the fruits of apple and other orchard trees (Figure 34–76). Other species in this genus attack cherries. The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), attacks citrus and other fruits, and often threatens to become a serious pest in the South. Species of the genus *Eurosta* form stem galls on goldenrod (Figure 34–78). The galls are rounded and thick-walled, with a single larva in the center. In the fall, the larva cuts a tunnel to the surface, overwinters as a larva in the gall, and pupates in the spring. In the larval stage, a few of the tephritids are leaf miners.

***Families* Ulidiidae and Platystomatidae—Picture-Winged Flies:** The picture-winged flies are a large group of small to medium-sized flies that usually have their wings marked with black, brown, or yellowish, and their body is often shining and metallic (Figure 34–79). They are usually found in moist places and are often very abundant. Little is known of their larval stages, but some feed on plants and occasionally damage cultivated plants, and some live in decaying materials. These groups are most abundant in the tropics, but there are 133 species of Ulidiidae and 41 species of Platystomatidae in North America.

***Family* Chamaemyiidae—Aphid Flies:** The chamaemyiids are small flies that are usually grayish, with black spots on the abdomen. The larvae of most species are predaceous on aphids, scale insects, and mealybugs. One species has been reared from birds' nests.

***Family* Lauxaniidae:** Lauxaniids are small, relatively robust flies, rarely over 6 mm long. Some have patterned wings, and they vary considerably in color. They can usually be distinguished from other acalyptrate muscoids by the complete subcosta, the lack of oral vibrissae, the postverticals converging, and the preapical tibial bristles. The group is a fairly large one (158 North American species), and its members are common in moist, shady places. The larvae live in decaying vegetation.

***Family* Coelopidae—Seaweed Flies:** The members of this family are medium-sized to small flies, usually dark brown or black, and have the dorsum of the thorax conspicuously flattened and the body and legs very bristly (Figure 34–80). These flies live along the seashore and are particularly abundant where various

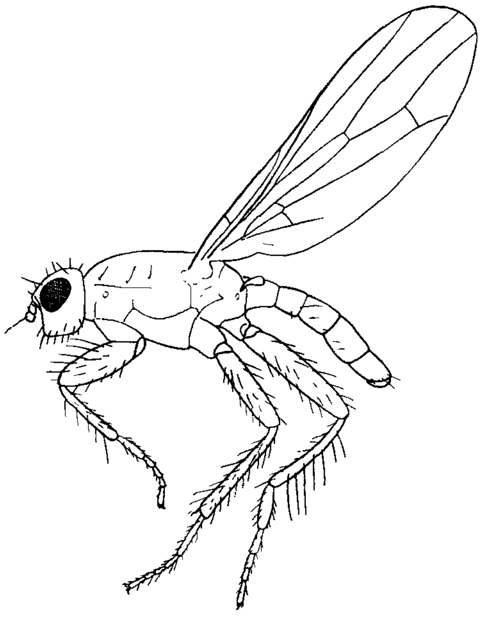


Figure 34–80 A seaweed fly, *Coelopa* sp. (Coelopidae).

seaweeds have washed up. The larvae breed in the seaweed (chiefly kelp) in tremendous numbers, mainly just above the high tidemark in seaweed that has begun to rot. The adults swarming over the seaweed often attract large numbers of shore birds, which feed on them. Seaweed flies feed on flowers and sometimes cluster so thickly on the flowers near the shore that a single sweep of a net can yield a hundred or more individuals. Four of the five North American species occur along the Pacific Coast. The other, *Coelopa frigida* (Fabricius), occurs along the Atlantic Coast from Rhode Island north.

***Family* Dryomyzidae:** This is a small group (11 North American species) of relatively rare flies that are similar to the Sciomyzidae. Three species in two genera (*Helcomyza* and *Heterocheila*, formerly placed in the family Helcomyzidae) occur along the Pacific coast from Oregon to Alaska. Their larvae live in rotting seaweed. The remaining species in the family are widely distributed and are usually found in moist woods. Their larvae live in decaying organic matter.

***Family* Ropalomeridae:** This is a small group of about 30 species, most occurring in Central and South America. They are of medium size and usually brownish or grayish, with the first posterior (R_5) cell narrowed apically, the femora thickened, and the hind tibiae often dilated. The only North American species, *Rhytidops floridensis* (Aldrich), occurs in Florida, where adults are usually found around fresh palm exudates.

***Family* Sciomyzidae—Marsh Flies:** The marsh flies are small to medium-sized flies that are usually yellowish or brownish and have the antennae extending forward (Figure 34–81). Many species have spotted or patterned wings and a characteristic bristle near the middle of the anterior face of the middle femur. This is a fair-sized group (nearly 191 North American species), and many species are common insects. They usually live along the banks of ponds and streams and in marshes, swamps, and woods. The larvae feed on snails, snail eggs, and slugs, generally as predators.

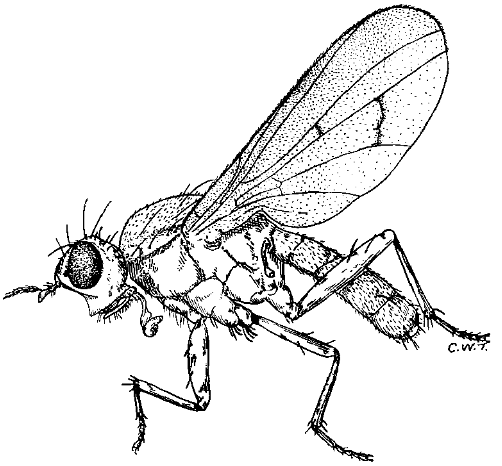


Figure 34–81 A marsh fly, *Tetanocera vicina* Macquart (Sciomyzidae), 7½×.

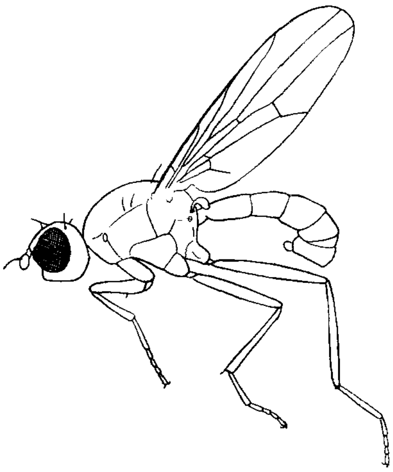


Figure 34–82 A black scavenger fly (Sepsidae), 15×.

***Family* Sepsidae—Black Scavenger Flies:** The sepsids are small, shining blackish flies (sometimes with a reddish tinge) that have the head spherical and the abdomen narrowed at the base (Figure 34–82). Many species have a dark spot along the costal margin of the wing near the tip. The larvae live in excrement and various types of decaying materials. The adults are common flies and are often found in considerable numbers near materials in which the larvae breed.

***Family* Acartophthalmidae:** This family is represented in North America by two rare species that have been taken on rotten fungi and carrion from Massachusetts to Oregon and Alaska. One of these, *Acartophthalmus nigrinus* (Zetterstedt), is about 2 mm long and is black with the front coxae and halteres yellow.

***Family* Agromyzidae—Leaf-Miner Flies:** These flies are small and usually blackish or yellowish (Figure 34–74B). The larvae are leaf miners, and the adults occur almost everywhere. Most species are more easily recognized by their mines than by the insects themselves. *Phytomyza aquilegivora* Spencer is a fairly common species that makes a serpentine mine in the leaves of wild columbine (Figure 34–83B). *Agromyza parvicornis* Loew makes a blotch mine in corn and several species of grasses. *Phytoliriomyza clara* (Melander) mines in the leaves of catalpa (Figure 34–83A). Most agromyzids make serpentine mines, that is, narrow, winding mines that increase in width as the larva grows. This is the largest family of acalyptrate muscoids, with over 700 North American species.

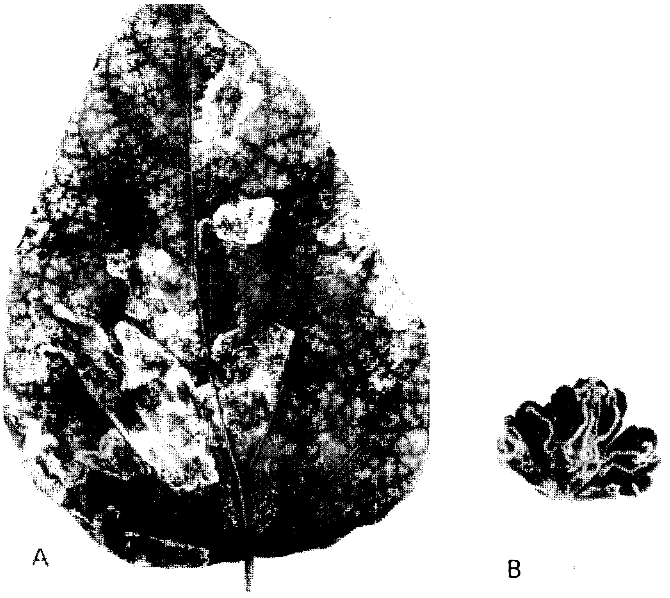


Figure 34–83 Leaf mines of agromyzid flies. A, the catalpa leaf-miner, *Phytoliriomyza clara* (Melander); B, the columbine leaf-miner, *Phytomyza aquilegivora* Spencer. (Courtesy of the Ohio Agricultural Research and Development Center.)

Family **Anthomyzidae:** These flies are small and somewhat elongate, and some species have pictured wings. This is a fairly small group (10 North American species), but its members are sometimes fairly common in grass and low vegetation, especially in marshy areas. The larvae live in marsh grasses and sedges.

Family **Asteiidae:** This family contains small to minute flies (usually 2 mm long or less), most of which can be recognized by the distinctive venation (Figure 34–24A): R_{2+3} ending in the costa close to R_1. In *Leiomyza*, R_{2+3} ends well beyond R_1, at about three fourths the wing length. Only 18 species occur in North America, and little is known of their habits.

Family **Aulacigastridae:** This group includes seven relatively rare species. *Aulacigaster leucopeza* (Meiger) is a small, blackish fly, about 2.5 mm long, with its face banded with white, brown, and orange. Adults live on (and larvae breed in) sap flows from tree wounds. The other species are yellowish to brownish and are generally found in grasses.

Family **Clusiidae:** The clusiids are small (mostly 3-4 mm long) and relatively uncommon flies in which the wings are often smoky or marked with brown, especially apically. The body color varies from pale yellow to black. In some species the thorax is black dorsally and yellowish laterally. The larvae, which live in decaying wood and under bark, can jump, much like the larvae of skipper flies.

Family **Odiniidae:** This is a small group of uncommon flies, formerly placed in the family Agromyzidae. They differ from the Agromyzidae in having preapical tibial bristles and patterned wings. The adults live at fresh sap flows on trees, about woody fungi, on rotting tree trunks and stumps, and in similar places. Eleven species occur in the United States, most of them in the East.

Family **Opomyzidae:** The opomyzids are small to minute flies that are usually found in grassy areas. The known larvae feed in the stems of various grasses. Only 13 species occur in North America, and most of these occur in the West or in Canada; none is common. Ten species of opomyzids are in the genus *Geomyza*, which has wings much narrowed at the base, without an alula and with no development of an anal lobe.

Family **Periscelididae:** The three North American species in this family are widely distributed but rare. They are usually found around the sap flowing from tree wounds. One species has been reared from fermenting oak sap.

Family **Braulidae—Bee Lice:** This family contains a single species, *Braula coeca* Nitzsch, which occurs in various parts of the world but is quite rare in North America. It is wingless and 1.2 to 1.5 mm long and is found in bee hives, usually attached to the bees. The adults apparently feed on nectar and pollen at the bee's mouth.

Family **Canacidae—Beach Flies:** The canacids are small flies that resemble the ephydrids in appearance and habits, but they have only a single break in the costa, they have an anal cell, and the ocellar triangle is quite large (as in Figure 34–27A). Adults of the seven rare North American species live along the seashore on both the East and West Coasts. The larvae live in the algae washed up on the shore.

***Family* Carnidae:** This small group (16 North American species) was formerly considered a subfamily of the Milichiidae. These flies can be separated from the Milichiidae by the characters in the key (couplet 135). One species, *Carnus hemapterus* Nitzsch, is a bloodsucking ectoparasite of birds.

***Family* Chloropidae—Grass Flies:** The chloropids are small, rather bare flies, and some species are bright yellow and black. They are very common in meadows and other grassy places, although they can be found in a variety of habitats. The larvae of most species feed in grass stems, and some are serious pests of cereals. A few are scavengers, and a few are parasitic or predaceous. Some of the chloropids (for example, *Hippelates*), which breed in decaying vegetation and excrement, are attracted to animal secretions and feed on pus, blood, and similar materials. They are particularly attracted to the eyes and are sometimes called "eye gnats." These flies can act as vectors of yaws and pinkeye. This is a fairly large group, with 290 North American species.

***Family* Cryptochetidae:** The flies in this group are somewhat similar to black flies (Simuliidae) and have habits similar to those of eye gnats (*Hippelates*, family Chloropidae: see preceding paragraph). They can usually be recognized by the enlarged third antennal segment, which reaches nearly to the lower edge of the head and which lacks an arista but bears at its apex a short spine or tubercle. As far as known, the larvae are parasites of scale insects in the family Margarodidae. This is principally an Old World group of flies, and only one species, *Cryptochetum iceryae* (Williston), occurs in the United States. It was introduced into California from Australia in the 1880s to control the cottony cushion scale, *Icerya purchasi*. This fly is about 1.5 mm long and stout-bodied, with dark, metallic blue head and thorax and shiny green abdomen. The introduction was successful. This fly is probably a more important natural enemy of the cottony cushion scale than the ladybird beetle, *Rodolia cardinalis*, which was also introduced from Australia to control this scale insect.

***Family* Milichiidae:** The milichiids are small flies, usually black or silvery, and are sometimes fairly common in open areas. The larvae generally live in decaying plant or animal materials. Many have a slender proboscis. This group is small, with 43 North American species.

***Family* Tethinidae:** Most tethinids are seashore species, living in beach grass, in salt marshes, and around seaweed washed up on the shore. The majority are found along the Pacific Coast. The inland species live mainly in alkaline areas. This is a small group (27 North American species), and its members are uncommon flies.

***Family* Chyromyidae:** This is a small (nine North American species) but widely distributed group of usually uncommon flies. Adults are usually taken on windows or on vegetation, and some have been reared from birds' nests and rotting wood.

***Family* Heleomyzidae:** The heleomyzids are a fairly large group (145 North American species) of small to medium-sized flies, most of which are brownish. Many superficially resemble marsh flies (Sciomyzidae), but they have well-developed oral vibrissae, converging postvertical bristles (Figure 34–23C), spinose costa (Figure 34–22H), and smaller and less prominent antennae. The adults are usually found in moist shady places. The larvae of most species live in decaying plant or animal matter or in fungi.

***Family* Sphaeroceridae—Small Dung Flies:** The sphaerocerids are very small, black or brown flies that can usually be recognized by the character of the hind tarsi (Figure 34–26A). Many have the longitudinal veins somewhat shortened and not reaching the wing margin (Figure 34–26D). This is a fair-sized group (250 North American species) whose members are common in swampy places near excrement. They often live in large numbers about manure piles. The larvae live in excrement and refuse.

***Family* Camillidae:** These flies resemble the Drosophilidae, but they are metallic, lack sternopleural bristles, they have the anal cell open apically. One species, *Camilla glabra* (Fallén), has been reported from Ontario. Nothing is known of its biology.

***Family* Curtonotidae:** This group is represented in North America by a single species, *Curtonotum helvum* (Loew), which occurs in the East. This species is about 6 mm long, *Drosophila*-like in appearance, and light yellowish brown with dark brown markings. It lives in high grass in moist places. The larva is unknown.

***Family* Diastatidae:** This is a small (six North American species) but widely distributed group whose members resemble the Drosophilidae but are usually dark-colored. They are relatively rare, and little is known of their habits.

***Family* Drosophilidae—Pomace Flies or Small Fruit Flies:** These flies are 3–4 mm long and usually yellowish (Figure 34–84), and they are generally found around decaying vegetation and fruits. This group is large (182 North American species), and many species are very common. The pomace flies are often pests in the household when fruits are present. The larvae of most species live in decaying fruits and fungi. The larvae actually feed on the yeasts growing in the fruits. A few species are ectoparasitic (on caterpillars) or predaceous (on mealybugs and other small Hemiptera) in the larval stage. Several species in this group, because of their short life span, giant salivary-gland chromo-

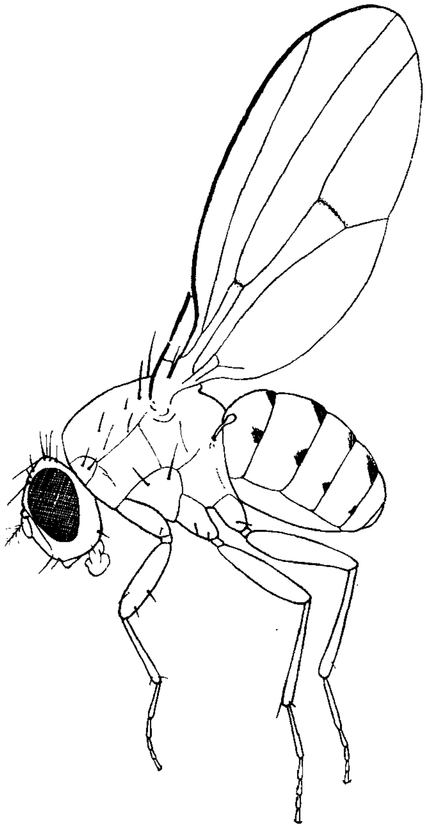


Figure 34–84 A pomace fly, *Drosophila* sp., 20×.

somes, and ease of culturing, have been used extensively in studies of heredity.

Family **Ephydridae—Shore Flies:** This is a large group (463 North American species), and some species are quite common. Shore flies are small to very small. Most are dark-colored, and a few have pictured wings. The adults are found in moist places: marshes, the shores of ponds and streams, and the seashore. The larvae are aquatic, and many species live in brackish or even strongly saline or alkaline water. One western species, *Helaeomyia petrolei* (Coquillett), breeds in pools of crude petroleum. These flies often occur in enormous numbers. Pools along the seashore can sometimes be alive with the adults, which walk or cluster on the surface of the water (for example, *Ephydra riparia* Fallén; Figure 34–85). Along the shore of Great Salt Lake, ephydrids can arise from the ground in clouds, and a few sweeps of a net can yield a cupful. At one time the Native Americans gathered the puparia from the lake and ate them.

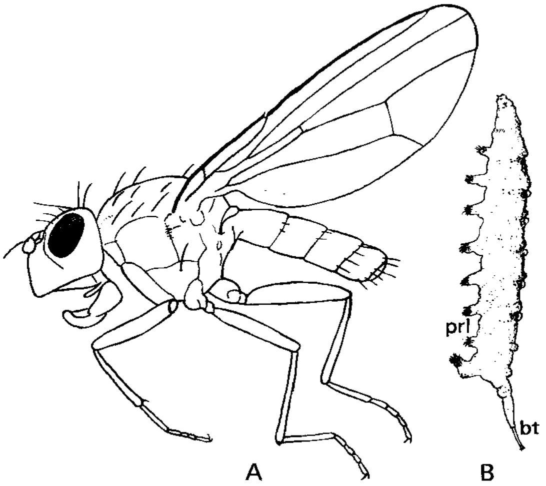


Figure 34–85 A shore fly, *Ephydra riparia* Fallén. A, adult, 10×; B, larva, 4×. *bt*, breathing tube; *prl*, prolegs. (B, courtesy of Peterson; reprinted by permission.)

Collecting and Preserving Diptera

The general methods of collecting Diptera are similar to those of collecting other insects. To obtain a large variety, one must collect in a variety of habitats. Many of the smaller species can be best collected by sweeping, putting the entire catch into the killing bottle, and examining it carefully later. Traps such as that shown in Figure 35–6B, using various types of baits, are useful collecting devices.

Most Diptera, particularly the smaller specimens, should be mounted within a few hours after they are captured because they dry quickly and are likely to be damaged in mounting if they have dried out very much. Many of the smaller and more delicate specimens, such as midges, mosquitoes, and similar forms, should be handled very carefully in order to avoid rubbing off the minute hairs and scales, which are often important in identification, particularly if the specimen is ever identified to species. The only way to get good specimens of many of these delicate forms is to rear them and to get them into a killing jar without using a net.

The larger Diptera are preserved on pins, and the smaller specimens are mounted on points, minuten pins, or microscope slides. In pinning a fly, particularly the muscoids, it is important that the bristles on the dorsum of the thorax be kept intact; insert the pin to one side of the midline. If the specimen is too small to pin this way, mount it on a point. Specimens mounted on a point should be on their right side, with the wings together above the body and lying along the point, and the body at right angles to the point (Figure 35–13). If a specimen to be mounted on a point dies with its wings bent down, the wings can often be snapped into the vertical position by gently squeezing the thorax with forceps. Do this as soon as possible after the insect dies. Some of the more minute specimens (especially Nematocera) should be preserved in fluids and must be mounted on microscope slides for detailed study.

References

Alexander, C. P. 1967. The crane flies of California. Bull. Calif. Insect Surv. 8:1–269.

Arnaud, P. H., Jr. 1978. A Host–Parasite Catalog of North American Tachinidae (Diptera). USDA Misc. Publ. 1319, 860 pp.

Ashe, P. 1983. A catalogue of chironomid genera and subgenera of the world including synonyms (Diptera: Chironomidae). Entomol. Scand. Suppl. 20, 68 pp.

Bickel, D. J. 1982. Diptera. In S. B. Parker (Ed.), Synopsis and Classification of Living Organisms, pp. 563–599. New York: McGraw-Hill.

Blanton, F. S., and W. W. Wirth. 1979. The sand flies (*Culicoides*) of Florida (Diptera: Ceratopogonidae). Arthropods of Florida and Neighboring Land Areas 10:1–204.

Borkent, A. 1993. A world catalogue of fossil and extant Crethrellidae and Chaoboridae (Diptera), with a listing of references to keys, bionomic information and descriptions of each known life stage. Entomol. Scand. 24:1–24.

Borkent, A., and W. W. Wirth. 1997. World species of biting midges (Diptera: Ceratopogonidae). Bull. Amer. Mus. Nat. Hist. 233:1–257.

Brown, B. V. 1992. Generic revision of Phoridae of the Nearctic region and phylogenetic classification of Phoridae, Sciadoceridae, and Ironomyiidae (Diptera: Phoridae). Mem. Entomol. Soc. Can. 164:1–144.

Carpenter, S. J., and W. J. La Casse. 1955. Mosquitoes of North America (North of Mexico). Berkeley: University of California Press, 360 pp.

Cole, F. R. 1969. The Flies of Western North America. Berkeley: University of California Press, 693 pp.

Courtney, G. W. 1991. Phylogenetic analysis of the Blephariceromorpha, with special reference to mountain midges (Diptera: Deuterophlebiidae). Syst. Entomol. 16:137–172.

Courtney, G. W. 1994. Biosystematics of the Nymphomyiidae (Insecta: Diptera): Life history, morphology, and phylogenetic relationships. Smithson. Contrib. Zool. 550, 41 pp.

Crosskey, R. W., and T. M. Howard. 1997. A New Taxonomic and Geographical Inventory of World Blackflies (Diptera: Simuliidae). London: Natural History Museum, 144 pp.

Cumming, J. M., B. J. Sinclair, and D. M. Wood. 1995. Homology and phylogenetic implications of male genitalia in Diptera, Eremoneura. Entomol. Scand. 26:120–151.

Curran, C. H. 1934. The Families and Genera of North American Diptera. New York: Author, 512 pp. (Reprinted by Henry Tripp, Mount Vernon, NY, 1965)

de Meyer, M. 1996. World catalogue of Pipunculidae (Diptera). Brussels Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen. 86, 172 pp.

DeSalle, R., and D. Grimaldi. 1992. Characters and the systematics of Drosophilidae. J. Heredity 83:182–188.

Disney, R. H. L. 1994. Continuing the debate relating to the phylogenetic reconstruction of the Phoridae (Diptera). G. Ital. Entomol. 7:103–117.

Evenhuis, N. L. 1999. World Catalog of Bee Flies (Diptera: Bombyliidae). Leiden: Backhuys, 756 pp.

Felt, E. P. 1940. Plant galls and gall makers. Ithaca, N. Y.: Comstock, 364 pp.

Friedrich, M., and D. Tautz. Evolution and phylogeny of the Diptera: A molecular phylogenetic analysis using 28S rDNA sequences. Syst. Biol. 46:674–698.

Gillette, J. D. 1971. Mosquitoes. London: Weidenfeld and Nicolson, 274 pp.

Griffiths, G. C. D. 1972. The phylogenetic classification of Diptera-Cyclorrhapha, with special reference to the male postabdomen. Series Entomologica 8:1–340.

Griffiths, G. C. D. 1994. Relationships among the major subgroups of Brachycera (Diptera): A critical review. Can. Entomol. 126:861–880.

Grimaldi, D. A. 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). Bull. Amer. Mus. Nat. Hist. 197:1–139.

Hall, D. G. 1948. The blow flies of North America. Thomas Say Foundation Publ. 4, 477 pp.

Harbach, R. E., and I. J. Kitching. 1998. Phylogeny and classification of the Culicidae (Diptera). Syst. Entomol. 23:327–370.

Hennig, W. 1948–1952. Die Larvenformen der Dipteren. Berlin: Akademie-Verlag, Part 1: 185 pp. (1948). Part 2: 458 pp. (1950). Part 3: 628 pp. (1952).

Huckett, H. C. 1965. The Muscidae of northern Canada, Alaska, and Greenland (Diptera). Mem. Entomol. Soc. Can. 42:1–369.

Hull, F. M. 1962. Robberflies of the world: The genera of the family Asilidae. U.S. Natl. Mus. Bull. 224 (2 vols.), 907 pp.

James, M. T. 1960. The soldier flies or Stratiomyidae of California. Bull. Calif. Insect Surv. 6(5):79–122.

Johannsen, O. A. 1910–1912. The fungus gnats of North America. Maine Agr. Expt. Sta. Bull., 172:209–279, 180:125–192, 196:249–327, 200:57–146.

Kessel, E. L., and E. A. Maggioncalda. 1968. A revision of the genera of Platypezidae, with descriptions of five new genera, and considerations of the phylogeny, circumversion, and hypopygia (Diptera). Weismann J. Biol. 26(1):33–106.

Knight, K. L., and A. Stone. 1973. A Catalog of the Mosquitoes of the World (Diptera: Culicidae), 2nd ed. College Park, MD: Thomas Say Foundation. Vol. 6, 611 pp. Supplement to Vol. 6 (1978, by K. L. Knight), 70 pp.

Maa, T. C. 1971. An annotated bibliography of batflies (Diptera: Streblidae, Nycteribiidae). Pac. Insects Monogr. 28:119–211.

Matheson, R. 1944. Handbook of the Mosquitoes of North America. Ithaca, NY: Comstock, 314 pp.; illus.

Mathis, W. M. 1992. World catalog of the beach-fly family Canacidae (Diptera). Smithson. Contrib. Zool. 536, 18 pp.

Mathis, W. M. 1996. World catalog of the family Tethinidae (Diptera). Smithson. Contrib. Zool. 584, 27 pp.

Mathis, W. M., and T. Zatwarnicki. 1995. World catalog of shore flies (Diptera: Ephydridae). Mem. Entomol. Intern. 4, 423 pp.

McAlpine, J. F. 1963. Relationships of *Cremifania* Czerny (Diptera: Chamaemyiidae) and description of a new species. Can. Entomol., 95(3):239–253.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1981–1987. Manual of Nearctic Diptera, Vol. 1, Monogr. No. 27, Ottawa: Research Branch, Agriculture Canada, 674 pp. (1981); Vol. 2, Monogr. No. 28, Ottawa: Research Branch, Agriculture Canada, pp. 675–1332. (1987).

McAlpine, J. F., and D. V. Wood. 1989. Manual of Nearctic Diptera, Vol. 3. Monogr. No. 32. Ottawa: Research Branch, Agriculture Canada, pp. 1333–1581.

McFadden, M. W. 1972. The soldier flies of Canada and Alaska (Diptera: Stratiomyidae). Part 1: Beridinae, Sarginae, and Clitellariinae. Can. Entomol. 104:531–561.

Moucha, J. 1976. Horse-flies (Diptera: Tabanidae) of the world. Synoptic catalogue. Acta Entomol. Mus. Nat. Prag. Suppl. 7, 319 pp.

Oldroyd, H. 1964. The Natural History of Flies. London: Weidenfeld and Nicolson, 324 pp.

Oosterbroek, P., and G. Courtney. 1995. Phylogeny of the nematocerous families of Diptera (Insecta). Zool. J. Linn. Soc. 115:267–311.

Oosterbroek, P., and B. Theowald. 1991. Phylogeny of the Tipuloidea based on characters of larvae and pupae (Diptera, Nematocera): with an index to the literature except Tipulidae. Tijdschr. Entomol. 134:211–267.

Pape, T. 1996. Catalogue of the Sarcophagidae of the world (Insecta: Diptera). Mem. Entomol. Intern. 8, 558 pp.

Pape, T. 2001. Phylogeny of Oestridae (Insecta: Diptera). Syst. Entomol. 26:133–171.

Pechuman, L. L. 1973. Horse flies and deer flies of Virginia (Diptera: Tabanidae). Va. Polytech. Inst. State Univ. Res. Div. Bull. 81, 92 pp.

Pennak, R. W. 1978. Fresh-Water Invertebrates of the United States, 2nd ed. New York: Wiley Interscience, 803 pp.

Peters, T. M., and E. F. Cook. 1966. The Nearctic Dixidae (Diptera). Misc. Publ. Entomol. Soc. Amer. 5(5):231–278.

Peterson, A. 1951. Larvae of Insects. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Ann Arbor, Mich.: Edwards, 416 pp.

Roback, S. D. 1951. A classification of the muscoid Calyptrate Diptera. Ann. Entomol. Soc. Amer. 44:327–361.

Sabrosky, C. W. 1937. On mounting micro-Diptera. Entomol. News 48:102–107.

Saether, O. A. 2000a. Phylogeny of Culicomorpha (Diptera). Syst. Entomol. 25:223–234.

Saether, O. A. 2000b. Phylogeny of the subfamilies of Chironomidae (Diptera). Syst. Entomol. 25:393–403.

Sinclair, B. J. 1992. A phylogenetic interpretation of the Brachycera (Diptera) based on the larval mandible and associated mouthpart structures. Syst. Entomol. 17:233–252.

Sinclair, B. J., J. M. Cumming, and D. M. Wood. 1993. Homology and phylogenetic implications of male genitalia in Diptera, lower Brachycera. Entomol. Scand. 24:407–432.

Skevington, J. H., and D. K. Yeates. 2000. Phylogeny of the Syrphoidea (Diptera) inferred from mtDNA sequences and morphology with particular reference to classification of the Pipunculidae (Diptera). Mol. Phylogenet. Evol. 16:212–224.

Spencer, K. A. 1969. The Agromyzidae of Canada and Alaska. Mem. Entomol Soc. Can. 64:1–311.

Steffan, W. A. 1966. A generic revision of the family Sciaridae (Diptera) of America north of Mexico. Univ. Calif. Publ. Entomol. 44:1–77.

Steyskal, F. C. 1967. A key to the genera of Anthomyiinae known to occur in America north of Mexico, with notes on the genus *Ganperda* (Diptera: Anthomyiidae). Proc. Biol. Soc. Wash. 80:1–7.

Stone, A. 1970. A synoptic catalog of the mosquitoes of the world, Supplement 4 (Diptera: Culicidae). Proc. Entomol. Soc. Wash. 72:137–171.

Stone, A., C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson. 1965. A catalog of the Diptera of America north of Mexico. USDA Agr. Handbook 276, Washington DC: USDA, 1969 pp.

Sublette, J. E. 1964. Chironomid midges of California. Part 2: Tanypodinae, Podonominae, and Diamesinae. Proc. U.S. Natl. Mus. 115:85–136.

Thompson, P. H. 1967. Tabanidae of Maryland. Trans. Amer. Entomol. Soc. 93:463–519.

Thompson, F. C. 2004. The BioSystematic Database of World Diptera. http://www.sel.barc.usda.gov/Diptera/biosys.htm. Accessed 25 March, 2004.

Tillyard, R. J. 1926. The Insects of Australia and New Zealand. Sydney: Angus and Robertson.

Vockeroth, J. R. 1969. A revision of the genera of the Syrphini (Diptera: Syrphidae). Mem. Entomol. Soc. Can. 62:1–176.

Wiegmann, B. M., C. Mitter, and F. C. Thompson. 1993. Evolutionary origin of the Cyclorrhapa (Diptera): Tests of alternative morphological hypotheses. Cladistics 9:41–81.

Wiegmann, B. M., S. C. Tsaur, D. W. Webb, D. K. Yeates, and B. K. Cassel. 2000. Monophyly and relationships of the Tabanomorpha (Diptera: Brachycera) based on 28S ribosomal gene sequences. Ann. Entomol. Soc. Amer. 93:1031–1038.

Wirth, W. W., and A. Stone. 1956. Aquatic Diptera. In R. L. Usinger (Ed.), Aquatic Insects of California, pp. 372–482. Berkeley: University of California Press.

Yeates, D. K. 1994. The cladistics and classification of the Bombyliidae (Diptera, Asiloidea). Bull. Amer. Mus. Nat. Hist. 219:1–191.

Yeates, D. K., and B. M. Wiegmann. 1999. Congruence and controversy: Toward a higher-level phylogeny of Diptera. Annu. Rev. Entomol. 44:397–428.

35 Collecting, Preserving, and Studying Insects

One of the best ways to learn about insects is to go out and collect them. Handling specimens and preparing collections will reveal many things that cannot be communicated in textbooks. Many people find collecting insects extremely interesting, because it provides not only the satisfaction that comes from being in the field, but also the satisfaction of learning at first hand. The student can develop much more interest in insects by collecting and handling them than by merely looking at pictures or preserved specimens. Seeing specimens alive enables the student to learn about their habitats, habits, and behavior—information often as valuable as morphological characters in determining their taxonomic position. Perhaps the greatest compliment that any entomologist, even a crusty professor, can receive is to be called a good field worker.

When and Where to Collect

In collecting insects—as with almost any activity—time and effort expended are directly correlated with proficiency gained. The uninitiated can stroll through habitats literally swarming with insects and be totally unaware of their presence. Few outdoor activities sharpen powers of observation and perception, test patience and skill, and provide never-ending sources of wonder and pleasure as well as collecting insects does.

Insects can be found practically everywhere and usually in considerable numbers. The more kinds of places you look for them, the greater the variety you can collect. The best time to collect is in summer, but insects are active from early spring until late fall, and many can be found in hibernation during the winter. Insects are active the year round in southern areas of the United States. The adults of many species have a short seasonal range, so anyone who wants to get the greatest variety should collect throughout the year. Because different species are active at different times of the day, at least some kinds of insects can be collected at any hour. Bad weather conditions, such as rain or low temperature, reduces the activity of many insects, making it more difficult to find or collect them, but others are little affected and can be collected in any kind of weather. If you know where to look, you can find insects in the average community at any hour of the day, any day of the year.

Because many kinds of insects feed on or frequent plants, vegetation provides one of the best places for collecting. Insects can be picked, shaken, or swept off the plant with a net. Different species feed on different kinds of plants, so examine all sorts of plants. Every part of the plant may harbor insects: Most will probably be on the foliage or flowers, but others may be on or in the stem, bark, wood, fruits, or roots.

Various types of debris often harbor many kinds of insects. Some species can be found in the leaf mold and litter on the surface of the soil, particularly in woods or areas where the vegetation is dense. Others can be found under stones, boards, bark, and similar objects. Still others can be found in rotting or decaying material of all sorts, such as fungi, decaying plants, the bodies of dead animals, rotting fruits, and dung. Many insects in these situations can be picked up with the fingers or forceps. Others can be obtained by sifting debris.

Insects can be found in or around buildings or on animals or humans. Many use buildings, cavities under buildings, culverts, and similar places as a shelter, and some species are most easily collected in such situations. Other insects found in buildings feed on clothing, furniture, grain, food, and other materials. Insects that attack animals are usually found around those animals, and a person interested in collecting species that attack humans can often get them with little effort—simply by letting the insects come to the collector.

On warm evenings, insects from various sources are attracted to lights and can be collected at street or porch lights, on windows or screens of lighted rooms, or at lights put up especially to attract them. This is one of the easiest ways of collecting many types of insects.

Many nocturnal insects, however, are not attracted to lights. You must search for them at night and capture them by hand. Examining tree trunks, leaves and other vegetation, fallen logs, rock faces, and other habitats at night will reveal a sizable arthropod fauna, unsuspected by those who only collect in daylight. Flashlights and lanterns of various sorts are useful for night collecting, but the best sort of light is a headlamp. Not only does it leave both hands free (you'll often wish that you had three or four extra arms and hands), but its beam also focuses your attention on smaller areas and sharpens your perception: The lamp illuminates only the area where you are looking. Get a headlamp with an elastic headband and operated by a 6-volt battery attached to the belt, available at almost any big outdoor gear store.

A great many insects—only the immature stages in some cases, and all stages in others—are found in aquatic situations. Different types of aquatic habitats harbor different species, and different insects can be found in different parts of any particular pond or stream. Some are found on the surface, others live on aquatic vegetation, others are attached to or are under stones or other objects in the water, and still others burrow in the sand or muck of the bottom. Many aquatic insects can be collected by hand or with forceps. Others are most easily collected with various types of aquatic collecting equipment.

The adults of many species are best obtained by collecting the immature stages and rearing them. This process involves collecting cocoons, larvae, or nymphs and maintaining them in some sort of container until the adults appear. It is often possible to get better specimens by this method than by collecting adults in the field.

Although many people view insects simply as pests to be removed or killed, remember that many statutes classify them as wildlife. Further, a number of species are formally designated as endangered or threatened and, as such, are protected not only from collecting but also habitat disturbance. It is usually necessary to procure permits from authorities to collect insects on public lands, such as state and national parks and forests. The requirements for such documents vary widely, and generally parks have greater restrictions. Obtain and submit applications for the necessary permits well in advance of a collecting trip. Transporting wildlife or wildlife products, including insects, across state and international boundaries is also regulated. For species listed in the Appendices of the Convention on International Trade in Endangered Species (CITES), permits are required for import or export. Any legitimate retailer selling imported insects should be able to provide the buyer with documentation that the specimens were collected legally in the country of origin. Imports of wildlife into the United States must also be declared to the U.S. Fish and Wildlife Service (FWS). Travelers entering or returning to the United States may interact with a number of agencies, each with distinct areas of authority and interest. The typical routine is that the specimens are declared on the entry form; a customs agent then directs the traveler to the inspectors from the USDA (U.S. Department of Agriculture). Declaration of importation to FWS is then made by filing the appropriate form. All the laws and regulations involved are constantly under review and revision, and it is the responsibility of the importer (the traveler) to know and follow them.

A common complaint heard regarding the burgeoning growth of regulations and paperwork in connection with insect collecting is that a car driving down the road kills large numbers of insects without any permit required. The dedicated student of entomology, however, is effectively prevented from collecting, even though the negative effect on the insect population is likely to be negligible. Remember, though, these laws and regulations are designed to control and prevent the real and ongoing decimation of wildlife populations, by both legal and illegal means, and the job of enforcement agents is not to individually interpret these rules, but to enforce them. Opportunities for comments on proposed regulations regularly arise, and concerned individuals should make their legitimate concerns known to the appropriate agencies. The fact that comment periods are open for a set of regulations is commonly disseminated widely on the list-serves that serve the entomological community.

Collecting Equipment

The minimum equipment necessary to collect insects is your hands and some sort of container for the specimens collected. However, you can do much better with a net and killing jar, or better yet with a backpack or shoulder bag containing some additional equipment. For general collecting, it is best to have at least the following items:

1. Insect net
2. Killing jars
3. Pillboxes containing cleansing tissue
4. Envelopes, or paper for making envelopes
5. Vials filled with preservative
6. Forceps
7. 10× hand lens
8. Sheet of plain white paper

Some of these items, particularly the killing jars, pillboxes, envelopes, and vials of preservative, are most easily carried in a backpack or fanny pack. Forceps and hand lens can be attached to a string around your neck and carried in a shirt pocket. Strictly speaking, a hand lens is not a means of collecting, but it is useful for examining insects in the field.

Other items of value for some types of collecting are as follows:

9. Aspirator
10. Beating umbrella or sheet
11. Sifter
12. Traps
13. Aquatic collecting equipment
14. Headlamp (for night collecting)
15. Sheath knife
16. Camel's-hair brush

Insect Net

Insect nets can be purchased from a supply house or can be homemade. Homemade nets are fairly easy to make and are much less expensive. However, a good commercial net generally survives physical abuse much better. Handles made of aluminum are both light and strong. The length of the handle is generally about 3 feet, but some modular designs let the user increase the length up to 10 feet (or more). Collapsible heads allow the entire net to be stored very compactly. However, the flexibility in the rim may make such nets less suitable for sweeping through heavy vegetation. A net for general collecting should have mesh open enough that an insect can be seen through it. Finer weaves are necessary for smaller insects.

A net used with care will last a long time. Keep it away from stout thorns and barbed wire (to avoid tearing), and keep it dry. Insects caught in a wet net are seldom fit for a collection, and moisture eventually rots the net fabric.

When collecting with a net, you can work in either of two general ways: You can look for particular insects and then swing at them, or you can sweep (simply swing the net back and forth, usually through vegetation). The former method is usually used for collecting the larger insects and often demands a certain amount of speed and skill. The latter method produces a much greater quantity and variety of insects, although it may occasionally damage some delicate specimens.

When a particularly active insect is caught, use certain precautions to prevent the insect from escaping before it can be transferred to the killing jar. The safest method is to fold the net over with the insect in the bottom of the net (Figure 35–1). Then grasp the insect through the net (provided it is not one that stings) and transfer it to the killing bottle. If the insect is one that stings (when in doubt, assume that it *does* sting), there are three ways to transfer it to the killing bottle: (1) You can put the fold of the net containing the insect into the killing bottle until the insect is stunned, then pick the insect out of the net and put it into the bottle. (2) You can grasp the insect through the net with forceps, rather than with your fingers, and transfer it to the bottle. (3) You can get the insect into a fold of the net, stun it by pinching the thorax, and then transfer it to the killing bottle. The first method is probably the best.

Sweeping is the best way for the general collector to obtain the greatest number and variety of insects. After sweeping, you may wish to save the entire catch or only certain specimens. It is preferable to transfer the entire catch to the killing jar and *later* discard any specimens you don't want. The best way to save the entire catch is to shake the insects into the bottom of the net and then place this part of the net in the killing jar (a wide-mouthed jar is best), which is then closed until the insects are stunned. Then dump the net contents onto a sheet of paper (in a protected area out of the wind), re-

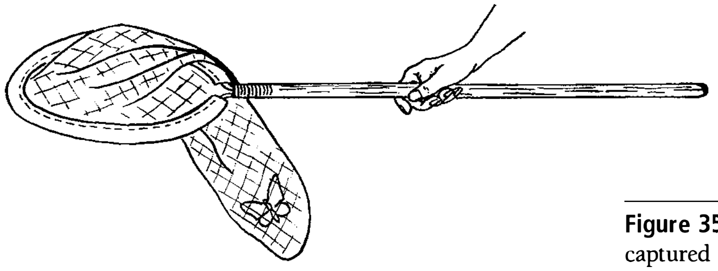


Figure 35–1 An insect net turned to prevent escape of captured specimens.

move by hand the larger pieces of vegetation or other debris, and dump the remainder into the killing jar. Once you have emptied the results of sweeping onto the sheet of paper, you can pick out the specimens (in the field) that you want to save, but it is better to save the entire catch and do the sorting after returning from the field. If you examine the results of sweeping under a binocular microscope, you may find (and save) many interesting insects that would otherwise be overlooked.

Another way to get the results of sweeping (or an individual insect) from the net to the killing jar is to insert the killing jar into the net. This procedure may save time compared with the method just described, but it seldom gets *all* the material taken in sweeping, and sometimes individual insects may escape. Work the insects into the bottom of the net with a few swings, and pinch off the net just above them. Then hold the tip of the net up (many insects tend to move upward to escape), insert the killing jar into the net (with the lid removed), quickly move it past the pinched-off point, and work the specimens into the jar. The jar may be capped from the outside long enough to stun the insects, or you can work it to the open end of the net (with the lid over the jar outside the net), then remove the lid from the outside and cap the jar. Some insects may escape with this method, but a little experience minimizes the losses.

Sweeping is often the only practical method of capturing small or minute insects. Because of their size, however, these specimens tend to dry out very rapidly, and the appendages, particularly the antennae, are subject to extensive breakage. One way to avoid this problem is to dump the entire contents of the net into a plastic bag (a 1-gallon food storage bag works well) filled about a quarter to a third full of water and with one or two drops of liquid detergent (or any other surfactant) added. The detergent reduces the surface tension of the water so that the insects are quickly wetted and drown. Specimens may be kept in the water for periods up to several hours. As soon as possible, however, thoroughly wash them in fresh water and then transfer them to 70% alcohol. This transfer can be made as the specimens are sorted (the same day they are caught). If you don't have enough time right away, you can pour the catch from the plastic bag into small mesh bags (made of the same fine material as the sweeping net). Then close the mesh bag with a twist tie, and place it in a container of alcohol. After 24 hours, drain the bag and place it in fresh alcohol. You can then sort specimens at your leisure. This method works well for collecting minute parasitic Hymenoptera and small beetles, for example, but it may not be appropriate for some other groups. Small flies may have the taxonomically important bristles broken off, and many mirids lose their hind legs when placed in alcohol.

Killing Bottles

If the insect is to be preserved after it is captured, it must be killed in such a way that it is not injured or broken. Some sort of killing bottle is thus required. Bottles of various sizes and shapes can be used, depending on the type of insects involved, and a number of different materials can be used as the killing agent. In the field it is generally desirable to have two or three killing bottles of different sizes for insects of different types. Always use a separate jar for Lepidoptera, because other insects (especially beetles) may damage their delicate wings and because their wing scales come off and adhere to other insects (making them look dusty). It is desirable to have one or more small bottles (perhaps 25 mm in diameter and 100–150 mm in length) for small insects and one or more larger bottles for larger insects. Corked bottles are preferable to screw-capped bottles, but either type will do. Wide-mouthed bottles or jars are better than narrow-necked ones. All killing bottles, regardless of the killing agent used, should be conspicuously labeled "POISON," and all glass bottles should be reinforced with tape to prevent shattering and spilling of the poisonous chemicals.

Several materials can be used as the toxic agent in a killing bottle. The traditional killing jar, preferred by many entomologists, uses cyanide. Such bottles kill quickly and last a long time, whereas most other materials kill more slowly and do not last as long. However, cyanide is extremely poisonous. But with certain precautions, bottles made with it can be just as safe as bottles made with some other killing agent.

Cyanide bottles can be made in two general ways (Figure 35–2). Those made with small vials have a plug of cotton and a piece of cardboard to hold the cyanide in the bottle, whereas those made with larger jars have plaster of paris holding the cyanide in the bottle. Sodium or potassium cyanide is the cyanide used in most cyanide bottles. Calcium cyanide is sometimes used in killing bottles made with small vials.

A calcium-cyanide killing bottle is made as shown in Figure 35–2A. Pack the cotton and cardboard down tightly, and put some pinholes in the cardboard. To reduce the hazard of breakage, reinforce the bottom and rim of the bottle with tape. If the killing bottle is capped with a large cork, it may be convenient to put the cyanide in a hole in the bottom of the cork and keep it there with a plug of cotton and a covering of cloth. Calcium cyanide is a dark gray powder that is often used as a fumigant. It is extremely poisonous. It should be handled with great care, and only people familiar with its properties should use it. This type of bottle is ready for use as soon as it is prepared.

A cyanide bottle made with plaster of paris takes longer to prepare but lasts longer. A bottle made with

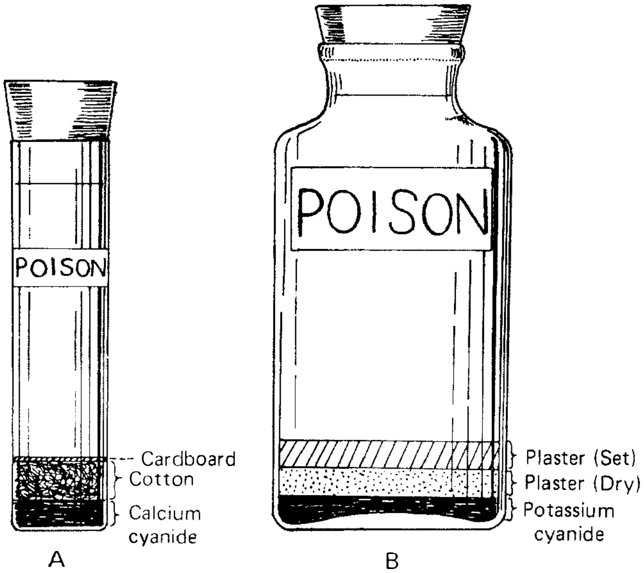


Figure 35–2 Cyanide bottles. A, small bottle made up with calcium cyanide; B, large bottle made up with plaster of paris.

calcium cyanide lasts a month or two, whereas one made with sodium or potassium cyanide and plaster lasts a year or two. The potassium (or sodium) cyanide should be in finely granular or powdered form, and the bottle is made as shown in Figure 35–2B. After pouring in the wet plaster, leave the bottle uncorked, preferably outdoors in a safe and ventilated place, until the plaster has thoroughly set and dried (a day or two). Then cork it, tape the bottom, put on a POISON label, and after another day or so for the cyanide to penetrate the now-dried plaster, it is ready for use.

Other materials that have been used as killing agents in insect bottles include ethyl acetate, carbon tetrachloride, and chloroform. Ethyl acetate is the least dangerous of the three. Bottles using these materials are made by putting some sort of absorbing material in the bottle and soaking it with the agent. Cotton makes a good absorbent material, but if it is used cover it with a piece of cardboard or screen, or the insects become entangled in the cotton and are difficult or impossible to remove without damage. If ethyl acetate or carbon tetrachloride is used, the absorbent material can be plaster of paris that has been mixed with water, poured into the bottom of the bottle, and allowed to set and thoroughly dry. Killing bottles made with these materials do not last very long and must be recharged frequently. Carbon tetrachloride and chloroform are poisonous, and people should avoid breathing the fumes. Ethyl acetate is relatively nontoxic to humans (it is an ingredient of nail polish).

The efficiency of a killing bottle depends to a large extent on how it is used. Never leave it uncorked any longer than is necessary to put insects in or take them out. The escaping gas reduces its strength, and an uncorked bottle (particularly one made with cyanide) is a hazard. Keep the inside of the bottle dry. Bottles sometimes "sweat"; that is, moisture from the insects (and sometimes from the plaster) condenses on the inside of the bottle, particularly if exposed to bright sunlight. Such moisture ruins delicate specimens. It is a good idea to keep a few pieces of cleansing tissue or other absorbent material in the bottle at all times, to absorb moisture and to prevent the insects from getting badly tangled up with one another. Change this material frequently, and wipe out the bottle periodically. A bottle that has been used for Lepidoptera should not be used for other insects unless it is first cleaned to remove scales that would get on new insects put into the bottle.

Other Types of Collecting Equipment

Aerial nets such as those already described are standard collecting equipment for most work, but many other devices are useful in certain situations or for collecting certain types of insects. Some of the more important of these are described here. With a little ingenuity, the collector will be able to devise many others.

Aspirator. This is a very useful device for capturing small insects, particularly if you want to keep them alive. Two types of aspirators are shown in Figure 35–3. Sucking through the mouthpiece draws small insects into the vial (A) or tube (B), and a cloth over the inner end of the mouthpiece tube prevents the insects from being sucked into the mouth. Nevertheless, the cloth will not significantly impede the passage of microorganisms or fungal spores that may be present in large

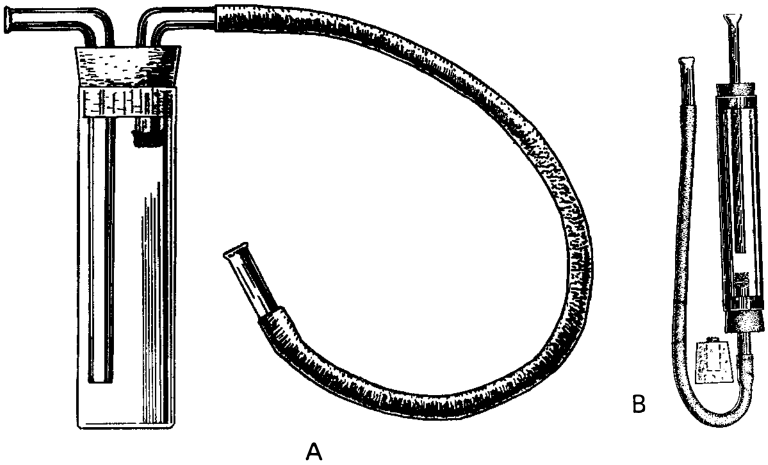


Figure 35–3 Aspirators. A, vial type; B, tube type. (B, from DeLong and Davidson 1936, courtesy of The Ohio State University Press.)

numbers on the substrate. With a series of these vials or tubes, an insect-filled one can be removed and replaced and with an empty one, and collecting can proceed with minimal interruption.

Beating Umbrella. Many insects that live on vegetation feign death by dropping off the plant when it is jarred slightly. The collector can take advantage of this habit by placing a collecting device underneath a plant and then jarring the plant with a stick. The insects that fall onto the collecting device beneath usually continue to play dead and can be easily picked up. The best device for this sort of collecting is a beating umbrella (Figure 35–4E), an umbrella frame covered with white muslin or light canvas. A white sheet, or even an open insect net, may also be used to catch insects jarred off a plant.

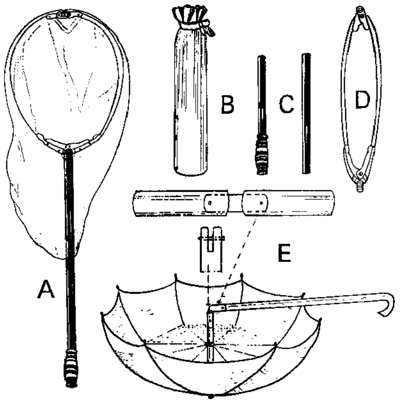


Figure 35–4 A collapsible net and beating umbrella. The net (A) may be collapsed (D), the handle removed and unjointed (C), and all these parts placed in a carrying bag (B). The beating umbrella (E) has a hinged joint in the handle and is held in the position illustrated when in use. (From DeLong and Davidson 1936, courtesy of the Ohio State University Press.)

Sifters. Many small and unusual insects that occur in trash and leaf litter are most easily collected by sifting. The simplest collecting procedure is to take a handful of material and sift it slowly onto a large piece of white cloth, plastic, or cardboard. The tiny animals falling onto the white surface reveal themselves by their movement and can be picked up with an aspirator or a wet brush. The material can also be sifted onto a white cloth from a small box with a screen bottom.

One of the most effective ways to get insects and other animals out of soil, debris, or leaf litter is to use a Berlese funnel (Figure 35–5). This is an ordinary, usually large, funnel containing a piece of screen or hardware cloth, with a killing jar or container of alcohol below it. The material to be sifted placed on the screen, and an electric light bulb is placed above the funnel. As the upper part of the material in the funnel dries, the insects and other animals move downward and eventually fall into the container below the funnel, where they are killed. A Berlese funnel is the best device for collecting debris-inhabiting insects, mites, pseudoscorpions, and small spiders.

Anyone using a Berlese funnel will notice that many of the animals collected (for example, the springtails and many of the mites) remain on the surface of the alcohol. The fact that many soil- and debris-inhabiting animals float on alcohol or water makes it possible to get many of these animals out of such materials by putting the material in water. Many animals come to the surface of the water, where they can be removed and placed in alcohol.

A Winkler funnel is similar in principle to a Berlese funnel, but is made of fabric in a slightly differ-

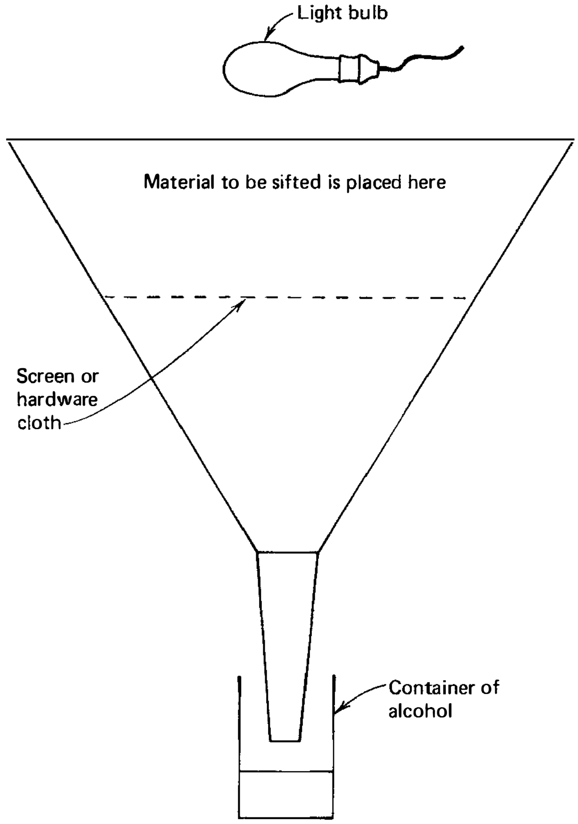


Figure 35–5 A Berlese funnel. The funnel can be supported by a ringstand, or by three or four legs attached near the middle of the funnel. The light bulb can be that of an ordinary gooseneck lamp, or it can be in a metal cylinder put over the top of the funnel. The material to be sifted is placed on the screen.

ent shape. It is much lighter and easier to transport in the field.

Traps. Traps are an easy and often very effective method of collecting many types of insects. A trap is any device, often containing something to which the insects are attracted, that is so arranged that once the insects get into it, they cannot get out. The attractant used and the general form of the trap are determined by the type of insects you want to collect. Space does not permit a description here of many types of traps, but a few can be mentioned. The ingenious collector can devise many that are not described.

A trap or other device using light as the attractant frequently yields insects in a quantity and quality not obtained by any other type of collecting. Black-light, ultraviolet, and mercury-vapor bulbs often attract more insects (or at least certain types of insects) than do ordinary light bulbs.

A light trap for insects may be made in such a way that insects coming to the trap are diverted, by a series of baffles, into a cyanide jar or container of alcohol (Figure 35–6D). Such a trap catches a lot of insects, but the specimens often are not in very good shape. Better specimens in better condition can be collected by simply waiting at a light and getting desired insects directly into a killing bottle or aspirator as they settle on something near the light (for example, a wall, screen, or sheet).

A particularly effective device that is very popular is the Malaise trap, named for Dr. René Malaise of Sweden (Figure 35–6C). Many modifications of this trap have been developed, but they are all essentially tentlike structures of fine netting into which flying insects wander. The underlying principle of this type of trap is that insects usually move upward in attempting to escape, and in the Malaise trap they eventually enter a collecting apparatus at the top of the trap and are killed in a jar of alcohol or one charged with cyanide or ethyl acetate. Such traps often turn up rare, unusual, or elusive insects not taken by collectors using conventional methods. Directions for building Malaise traps are given by Townes (1972).

Traps of the type shown in Figure 35–6B are useful for catching flies that are attracted to decaying materials such as meat and fruits. If the trap is visited frequently, the specimens it catches can be retrieved in good condition. Varying the bait produces a more varied catch.

Pitfall traps of the type shown in Figure 35–6A are useful for catching carrion beetles and other insects that do not fly readily. Such a trap may be made of a large plastic container, preferably with a few holes punched in the bottom to prevent water from accumulating in it, and with some sort of screen over the bait to permit easy removal of the insects caught. The trap is sunk into the ground with its top at ground level. Insects attracted by the bait will fall into the can and be unable to get out. The bait may be a dead animal, a piece of meat that will eventually decay, fruit, molasses, or some similar material. Here again, varying the bait yields a more varied catch.

Pan traps are similar in some respects to shallow pitfall traps. Place the pan (or bowl or any type of shallow container) on or sink it in the ground, and half-fill it with water to which a few drops of a liquid detergent have been added to reduce surface tension. Yellow pans are especially attractive to many species. The insects are either attracted to or inadvertently stumble into the trap, are wetted, and drown. Remove the catch from the pan with a small aquarium dip net. Traps containing only water must be tended every day to remove the

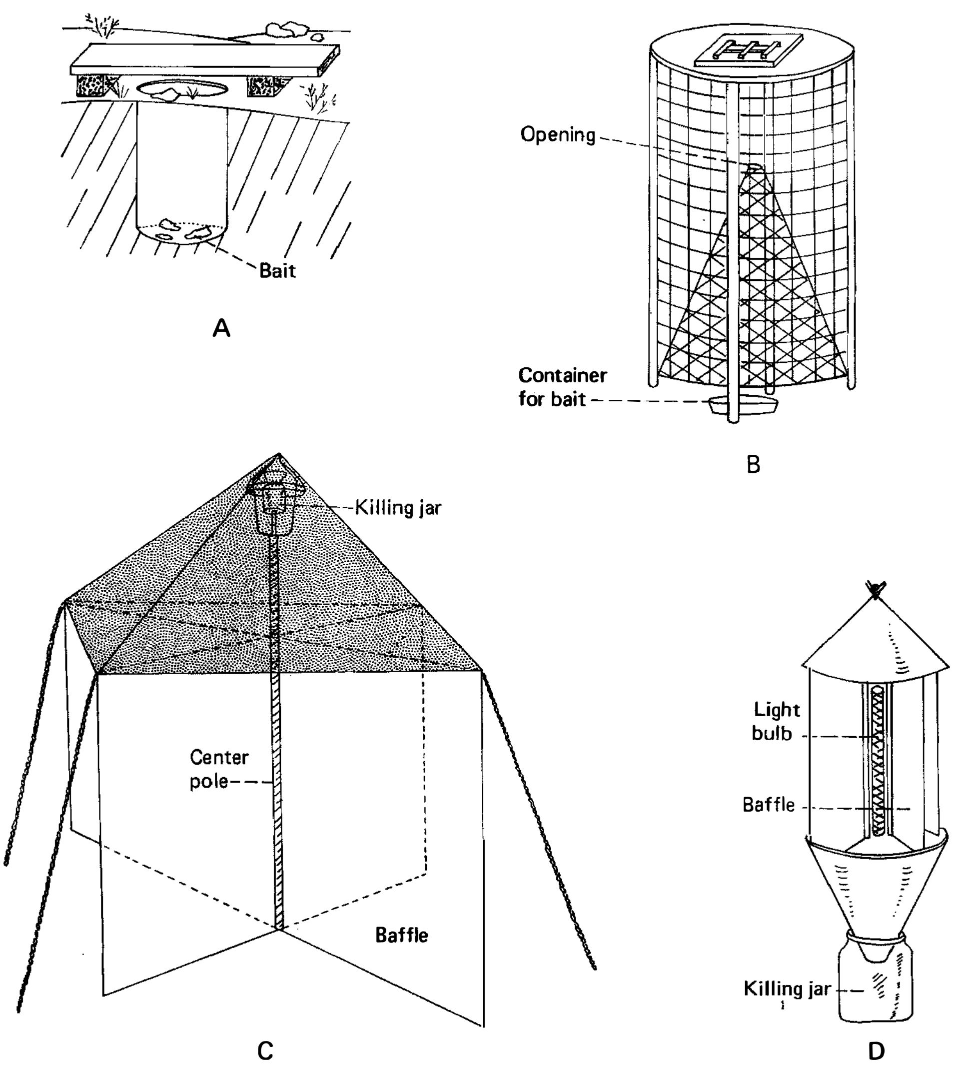


Figure 35–6 Insect traps. A, pitfall trap, consisting of a can sunk in the ground; B, fly trap, a cylindrical screen cage with a screen cone at the bottom; bait is placed in a container below the center of the cone, and flies attracted to the bait eventually go through the opening at the top of the cone into the main part of the trap, from which they can be removed through the door at the top; C, Malaise trap, a square, tentlike structure supported by a central pole, with screen or cloth baffles across the diagonals, and a killing jar at the top; D, light trap; specimens attracted to the light are funneled into the killing jar at the bottom.

insects before they decompose. Various preservatives can be added to the water to significantly delay decomposition. Filling the trap with water saturated with salt is an economical but somewhat bulky alternative (a great deal of salt is required). A 50–50 solution of propylene glycol (a food additive) and water also works well. Ethylene glycol, once commonly used in such traps, is easily accessible, particularly as antifreeze, but should be avoided because it is attractive and toxic to mammals. Traps that will not be tended for several days generally require some sort of roof over them (such as a suspended sheet of plastic) to keep the killing/preservative solution from being diluted by rainwater. Before placing them in alcohol, carefully and thoroughly rinse specimens in water. This is intended to remove any surfactant from the specimen as well as any material that the insect voided from its digestive tract when killed. Such materials coagulate on exposure to alcohol and are difficult or impossible to remove later. Pan traps are especially effective in catching minute insects that are found close to the ground where it is difficult to sweep.

Flight-intercept traps are in some ways a combination of Malaise and pan traps. Some insects, especially small ones, never reach the collecting apparatus at the top of a Malaise. They may crawl through the netting, fly off it before reaching the top, or fall off the trap to the ground. To catch these, place a trough, pan, or similar device filled with a killing/preservative fluid (such as those described earlier) beneath a single panel of fine netting spread across the flight path of the insects. A knock-down insecticide can be "painted" onto the fabric to capture specimens that may land on the netting. Designs for this type of trap can be found in Peck and Davies (1980) and Masner and Goulet (1981).

Household insects that do not fly, such as silverfish and cockroaches, can be trapped in an open-topped baited box. Place a box 100 or 125 mm deep on the floor, provide it with a ramp from the floor to the top of the box, and bait it with dog biscuits, crackers, or some similar materials. Coat the upper 50 to 75 mm of the box on the inside with petroleum jelly, so insects that get into the box can't crawl out.

Many insects can be caught by "sugaring," that is, preparing a sugary mixture and spreading it on tree trunks, stumps, or fence posts. Various mixtures may be used, but one containing something that is fermenting is probably the best. It may be made with molasses or fruit juices and a little stale beer or rum.

Aquatic Collecting Equipment. Many aquatic insects can be collected with fingers or forceps when you are examining plants, stones, or other objects in the water, but many more can be collected by using a dip net, strainer, dipper, or other device. A dip net can be made like an aerial net, but the collecting bag should be shallower (no deeper than the diameter of the rim) and much stronger. The handle should be heavy, and the rim should be made of 6- or 9-mm metal rod and securely fastened to the handle. The part of the bag that is attached to the rim should be of canvas, and it is desirable to have an apron of the same material extending down over the front of the bag. The rim need not be circular. Many collectors prefer to have the rim bent in the form of the letter D, to be able to drag it flat across the bottom. The bag may be made of heavy marquisette or bolting cloth. Strainers of the tea type, with a rim from 50 to 150 mm in diameter, are useful for aquatic collecting if they are not subjected to hard use. Dip nets or strainers can be used to collect free-swimming forms, forms on vegetation, and forms burrowing in the sand or muck of the bottom. A good catch can often be obtained in streams by placing the net or strainer at a narrow place in the current and then turning over stones or disturbing the bottom upstream from the net. Retrieving insects from the muck and debris collected in a net or strainer is not always easy, because most of them are not noticed until they move. A good way to locate them is to dump the contents of the net into a large, white, enameled pan with some water. Against the white background, the insects can be more easily located and picked out. The best device for collecting small free-swimming forms such as mosquito larvae or midge larvae is a long-handled white enameled dipper. Small larvae are easily seen against the white background of the dipper and can be removed with an eye dropper.

Other Equipment. The collector should have a sheet of plain white paper for transferring the results of sweeping from the net to the killing jar (as noted earlier). A large, heavy knife is useful for prying up bark, cutting open galls, or digging into various materials. A vial of insect pins is useful for pinning together mating pairs before they are put into the killing jar. A notebook and pencil should always be a part of the collector's gear. Collecting certain types of insects often requires special items of equipment. The amount and type of equipment a collector uses depend entirely on the sort of collecting he or she expects to do.

A global positioning system (GPS) receiver is fast becoming a required piece of equipment for the serious collector. This device calculates the latitude, longitude, and altitude by comparison of the radio signals received from a constellation of satellites in orbit. Under the best conditions, a GPS unit can achieve an accuracy measured in centimeters. This is valuable for surveying applications, but is generally not required for collecting purposes. Under normal conditions, accuracies of ±30 meters are easily achieved and sufficient. Measurements of elevation are generally less accurate and the error more significant from a biological point of view. Elevation is probably still best measured by an altimeter. One note of caution: The GPS unit will report its position to a very high level of apparent accuracy. As a rule of thumb, 1 degree of latitude or longitude at the equator is equivalent to 100 km, 1 minute = 1.7 km, and 1 second = 27 m. Although a GPS unit will gladly report a position in decimal degrees such as 48° 29.7345′ N, that last digit implies an accuracy of approximately ±17 cm, a value that is neither correct nor biologically relevant.

Remember that the radio signals from the satellites are affected by a variety of environmental conditions and, if high accuracy is desired, then take and average a number of measurements, or use a differential GPS (in which the readings from a mobile unit are compared to a fixed receiver at a well-known location). Finally, calculation of the geographic position depends on an internal mathematical representation of the shape of the Earth, a geodetic datum. Record the datum used along with the latitude and longitude.

Handling the Catch

A collector must learn by experience how long it takes for the killing bottles to kill an insect. Some insects are killed quickly, whereas others are very resistant to the killing agent. A mosquito in a strong cyanide bottle will be killed in a few minutes, whereas some of the snout-nosed beetles may remain alive in the same bottle for an hour or two. Keep the catch in the killing bottle until the specimens are killed, but not much longer. Some insects become discolored if left in too long, particularly in a bottle containing cyanide. It is advisable to remove insects within an hour or two after they are killed.

Specimens removed from the killing bottle in the field can be placed in pillboxes or paper envelopes for temporary storage. The pillboxes should contain some sort of absorbent material, such as cleansing tissue, that will reduce the bouncing around of the specimens during transportation and absorb excess moisture. Paper envelopes, either ordinary letter envelopes or triangular envelopes like that shown in Figure 35–7, are excellent for temporary storage of large-winged insects such as butterflies, moths, or dragonflies. These triangular envelopes can be made quickly from a sheet of notebook paper, and specimens will remain in good condition in them. Collecting data (see later) can be written on the outside before putting in the specimen.

Many insects can be killed by dropping them directly into 70–90% ethyl or isopropyl alcohol, where they can be stored nearly indefinitely. This method is used exclusively for many insects, such as very minute forms that are to be mounted on microscope slides for detailed study (springtails, lice, fleas, and some Coleoptera, Hymenoptera, and Diptera) and many soft-bodied insects that may shrivel when mounted dry (camel crickets, termites, mayflies, stoneflies, caddisflies, and others). In contrast, adult Lepidoptera and Odonata should not be placed in alcohol. If the facilities are available, the field catch can be stored temporarily in a refrigerator, or it can be frozen and kept for an extended period. Any collector will soon learn the best way to kill and preserve the various kinds of insects.

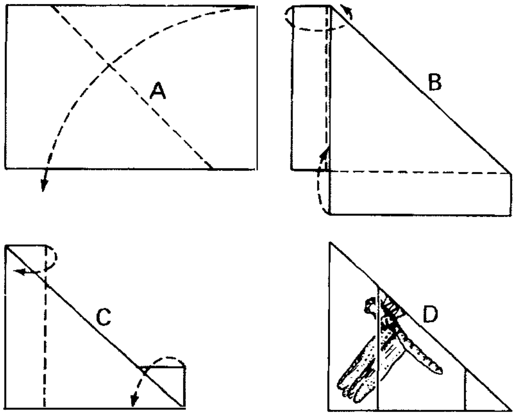


Figure 35–7 Folding triangular paper envelopes for insect specimens. Follow steps A, B, and C. (From DeLong and Davidson, courtesy of The Ohio State University Press.)

Process each day's catch as soon as possible. If specimens are to be pinned in the field, do the pinning before they become too stiff to handle without breaking off appendages. Many small insects dry extremely quickly. Process insects that are to be stored in paper envelopes (such as Odonata and Lepidoptera) while they are still soft enough to fold the wings above the body. Put specimens to be preserved in alcohol into the alcohol as soon as possible after they are killed, or kill them directly in it. Use a relatively large volume of alcohol, or after a day transfer the specimens into fresh alcohol to counteract the diluting effect of the insects' body fluids. Although alcohol significantly reduces the rate of decomposition, it does *not* stop it entirely. Specimens stored in alcohol continue to deteriorate over time, particularly in color. For this reason, keep material stored in alcohol in the dark and in cold conditions, such as a freezer.

It is extremely important to associate each lot of insects collected with a data label indicating at least the place and time of the collection and the name of the collector. Any other relevant data, such as elevation, habitat, collecting method, and what the insect was doing, should also be included. A specimen without such data may perhaps be better than no specimen at all—but not much! A specimen with incorrect data is even worse and creates problems for later researchers, especially systematists who place considerable importance on the data accompanying specimens. In most instances, only the collector can supply such data, and the longer he or she waits to label the catch, the greater the chance for errors in the labeling. It is advisable to not only include the information with the sample collected, but also to record the data in your own bound notebook. There, any additional details on the collection can be saved without limits on writing space. See the later section on labeling for guidelines for preparing the data labels that should accompany each insect specimen.

Mounting and Preserving Insects

Insects can be mounted and preserved in various ways. Most specimens are pinned, and, once dried, these keep indefinitely. Specimens too small to pin can be mounted on points, on tiny minuten pins, or on microscope slides. Large and showy insects, such as butterflies, moths, grasshoppers, dragonflies, and others, may be mounted in various types of glass-topped display boxes. Preserve soft-bodied forms (nymphs, larvae, and many adults) in fluids.

Relaxing

Mount all insects as soon as possible after they have been collected. If they are allowed to dry, they become brittle and are easily broken in the process of being mounted. Specimens stored in pillboxes or envelopes for a long time must be relaxed before they are mounted. Relaxing may be accomplished with a relaxing chamber or a special relaxing fluid, or sometimes hard-bodied insects such as beetles can be relaxed enough to pin by dropping them in hot water for a few minutes.

A relaxing chamber can be made of any wide-mouthed can or jar that can be made airtight. The bottom of the jar is covered with wet sand or cloth (preferably with a little phenol added to prevent mold); the insects are put in the jar in open, shallow boxes; and the jar is tightly closed. Special jars for this purpose can also be obtained from supply houses. The collector must learn by experience how long it takes to relax an insect, but after a day or two in such a chamber specimens are usually sufficiently relaxed to mount.

Entire specimens, or parts thereof, can often be relaxed by dipping them in a relaxing fluid for several minutes. The formula for this fluid (sometimes known as Barber's fluid) is as follows:

95% ethyl alcohol	50 ml
Water	50 ml
Ethyl acetate	20 ml
Benzene	7 ml

Another way to relax a specimen is to inject tap water into it with a hypodermic syringe (with a 20- or 25-gauge needle). Insert the needle into the thorax under the wings, and completely fill the thorax with water. This method is particularly useful for Lepidoptera (except small ones) that have been kept in paper envelopes. After injection return the specimen to the envelope for 5 to 20 minutes, after which it should be relaxed enough to mount.

Cleaning Specimens

It is seldom necessary to clean specimens, and it is usually better not to. A little dirt is preferable to a damaged specimen. Cleaning specimens is most likely to be desirable when they have been collected from mud, dung, or a similar material, some of which has stuck to the specimens. The easiest way to remove this material is to put the specimens in alcohol or in water to which a detergent has been added. If the material to be removed is greasy, cleaning fluid can be used.

Dust, lint, Lepidoptera scales, and the like can be removed by means of a camel's-hair brush, either dry or dipped in a cleaning fluid. This method can also remove films of oil or grease that sometimes exude from pinned specimens. Ultrasonic cleaners clean specimens quickly and thoroughly. Take care not to overdo ultrasonic cleaning, as the vibrations eventually break most specimens apart.

Pinning

Pinning is the best way to preserve hard-bodied insects. Pinned specimens keep well, retain their normal appearance, and are easily handled and studied. The colors often fade when the insect dries, but this fading is difficult to avoid under any circumstances. Bright colors are generally better preserved if the specimens are dried rapidly.

Common pins are undesirable for pinning insects. They are too thick, too short, and they rust. Insects should be pinned with a special type of steel pin known as an *insect pin*. These pins are longer than common pins, they can be obtained in various sizes (thicknesses), and they should not rust. Insect pin sizes range from 00 to 7. Number 2 or 3 pins are best for general use; the smaller sizes (that is, smaller in diameter) are too slender for all but specialty purposes. Size 7 pins are longer than the other sizes (and will not fit in some insect boxes or drawers); these pins are used in pinning very large insects, such as some tropical beetles.

Insects are pinned vertically through the body as shown in Figures 35–8 and 35–9. Bees, wasps, flies, butterflies, and moths are pinned through the thorax between the bases of the front wings. With flies and wasps, insert the pin a little to the right of the midline. Pin bugs through the scutellum (Figure 35–8C), a lit-

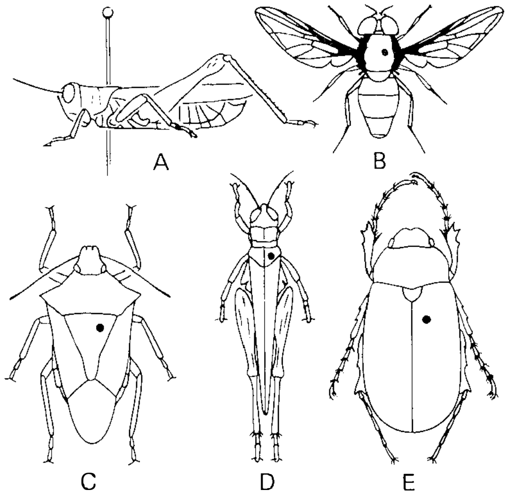


Figure 35–8 Methods of pinning insects. A, lateral view of a pinned grasshopper; black spots in the other figures show location of pin for flies (B), bugs (C), grasshoppers (D), and beetles (E). (Courtesy of the Illinois Natural History Survey.)

tle to the right of the midline if the scutellum is large. Grasshoppers are usually pinned through the posterior part of the pronotum, just to the right of the midline (Figure 35–8D). Pin beetles, earwigs, and large hoppers through the right fore wing, about halfway between the two ends of the body (Figure 35–8E). The pin should go through the metathorax and emerge through the metasternum (see Figure 26–4) so as not to damage the bases of the legs. Dragonflies and damselflies are best pinned horizontally through the thorax, with the left side uppermost. This method reduces the space necessary to house the collection, and a specimen so pinned can be studied just as easily as one pinned vertically. If the specimen does not have wings together above its back when it dies, move the wings into that position and put the specimen into an envelope for a day or so until it has dried enough for the wings to remain in this position. Then carefully pin it through the upper part of the thorax, below the base of the wings.

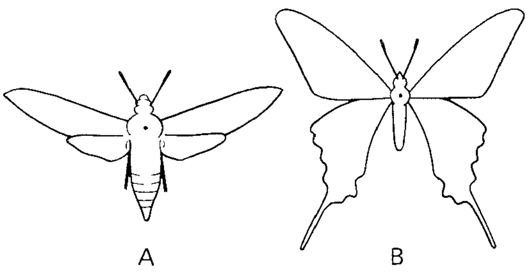


Figure 35–9 Pinning Lepidoptera. These insects are pinned through the center of the thorax, in both moths (A) and butterflies (B). (Courtesy of the Illinois Natural History Survey.)

The easiest way to pin an insect is to hold it between the thumb and forefinger of one hand and insert the pin with the other. Mount all specimens at a uniform height on the pin, about 25 mm above the point, but leave enough of the pin above the insect (for example, with heavy-bodied insects) to permit a comfortable finger hold. Uniformity can be obtained with a pinning block. There are a number of designs of pinning blocks (Figure 35–10); a common type (Figure 35–10A) consists of a block of wood in which three small holes have been drilled to different depths, usually 25, 16, and 9.5 mm.

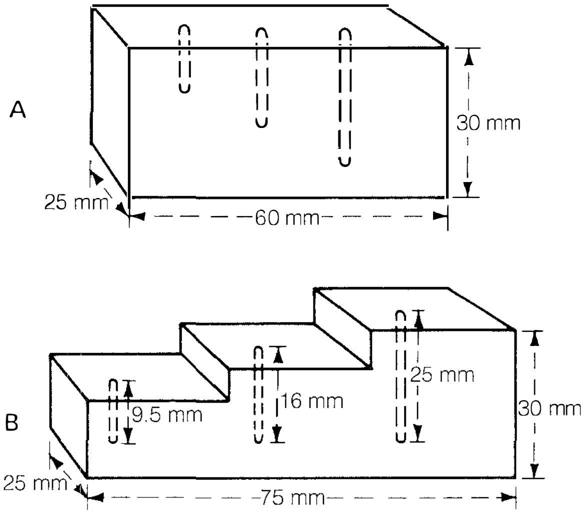


Figure 35–10 Pinning blocks. These can be rectangular pieces of wood containing holes drilled to different depths (A), or blocks shaped like stair steps, with holes drilled to the bottom (B). The block of the type shown in A usually has the holes drilled to depths of 25, 16, and 9.5 mm. After placing a specimen or label on the pin, insert the pin into the appropriate hole until it touches bottom—into the deepest hole for the specimen, the middle hole for the label bearing the locality and date, and the last hole for any additional label. For thick-bodied insects, leave enough room above the insect to grasp the pin. (From DeLong and Davidson 1936, courtesy of The Ohio State University Press.)

If the abdomen sags when the insect is pinned, as it sometimes does, stick the pinned specimen on a vertical surface with the abdomen hanging down and leave it there until it dries. If the insect is pinned on a horizontal surface, place a piece of stiff paper or cardboard on the pin beneath the insect to support it until it dries. Another alternative is to support the abdomen from below with a pair of crossed pins.

The appendages of a pinned insect need not be in a lifelike position (although the appearance of the collection is greatly improved if they are), but it is desirable to have them project out from the body slightly so they can be easily examined. The legs should be extended enough so that all parts are easily visible, and the wings should be extended out from the body so that the venation can be seen. Pinned bees that have the tongue extended are easier to identify than those with the tongue folded tightly against the underside of the head. The most important point to remember is that all such manipulations of the specimen are best done while the insect is still fresh and flexible.

Entomologists use various types of mounting boards to position the appendages of insects while they dry. These can be made of balsa wood, cork, Styrofoam, cardboard, or any soft material that allows a pin to be inserted deeply enough for the lower surface of the specimen to rest on a flat surface. Pins can then be used to arrange the legs, antennae, or other parts in any position desired and hold them there until the specimen dries. Once you become familiar with the characters used in identification in various groups, you can arrange and prepare your specimens accordingly.

A sheet of cork, balsa wood, or other soft material is very useful for temporary storage of pinned insects until they can be sorted and put into boxes. If you plan to use such temporary storage, be sure to read the section on collection pests.

Spreading Insects

When the specimen is pinned, the position of the legs or wings does not greatly matter as long as all parts can be easily seen and studied. With moths, butterflies, and possibly some other insects, and in the case of insects mounted in display boxes (see the following), the wings should be spread before the insect is put into the collection. The method of spreading depends on whether the specimen is mounted pinned or unpinned, and the position into which the wings should be put depends on the type of insects.

An insect that is to be part of a pinned collection is spread on a spreading board (Figure 35–11). Spreading boards can be obtained from a supply house or made at home. An insect to be mounted under glass, as in a Riker or glass mount, may be spread on any flat surface such as a piece of corrugated cardboard or a sheet of cork or balsa wood. When using a spreading board, the insect is ordinarily spread dorsal side up, and the pin is left in the insect. A specimen spread on a flat surface for a Riker mount is spread in an upside down position, and the pin is *not* left in the body of the insect.

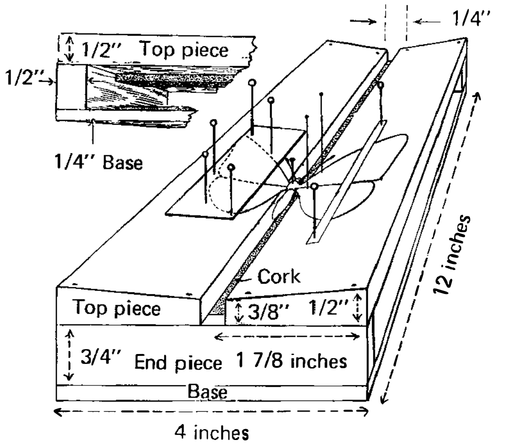


Figure 35–11 The spreading board, showing dimensions, details of construction (inset), and a spread specimen. The wings of the specimen can be held in place by a single, broad strip of paper as shown on the left wings, or by a narrower strip and pins as shown on the right wings. (Courtesy of the Illinois Natural History Survey.)

There are standard positions for the wings of a spread insect. In the case of butterflies and moths (many figures in Chapter 30) and mayflies (Figure 9–1), the rear margins of the front wings should be far enough forward so there is no large gap at the side between the front and hind wings. With grasshoppers, dragonflies, damselflies, and most other insects, the front margins of the hind wings should be straight across, with the front wings far enough forward that they just clear the hind wings. The front and hind wings of a butterfly or moth are always overlapped, with the front edge of the hind wing *under* the rear edge of the front wing. With other insects the wings are usually not overlapped.

The actual process of spreading an insect is relatively simple, through it requires a little practice to become proficient. Great care must be taken to not damage the specimen. Butterflies and moths must be handled with particular care to avoid rubbing off the scales on the wings; handle these insects with forceps. If the specimen is to be mounted on a spreading board, it is first pinned (like any other pinned insect), and then the pin inserted in the groove of the spreading board until the base of the wings is flush with the surface of the board. If the specimen is to be upside down on a flat surface, the pin is inserted into the thorax from underneath, and the insect is pinned on its back on some flat surface. It is often advisable to place pins along each side of the body to prevent it from swinging out of line.

The steps in spreading a butterfly are shown in Figure 35–12. Move the wings into position by pins and hold them there by strips of paper or other material pinned to the board, and orient the antennae and hold them in position by pins. Maneuver the wings by pins from near the base of the wing, along the front margin. The veins are heavier at this point, and there is less likelihood of tearing the wing. Do not put the pin through the wing if you can avoid it, because doing so leaves a hole. The specimen should be fastened down securely, and it may sometimes be necessary to use more strips of paper than are shown in Figure 35–12. This figure illustrates a method of spreading an insect upside down on any flat surface, and the final step in this process is to hold the body down with forceps and carefully remove the pin (G). If the specimen is spread on a spreading board, the steps are similar, but the pin is left in the specimen.

The length of time it takes a spread specimen to dry depends on the size of the specimen and such other

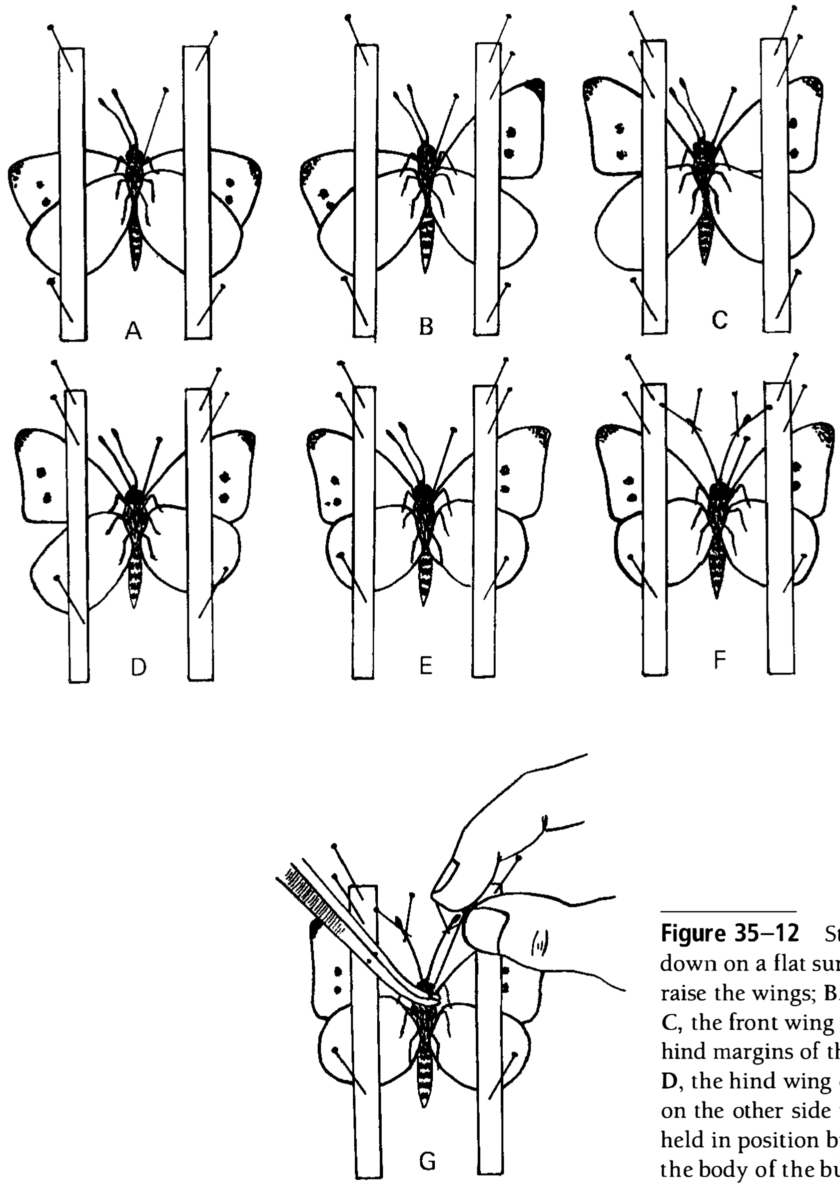


Figure 35–12 Steps in spreading a butterfly upside down on a flat surface. A, position before starting to raise the wings; B, the front wing on one side raised; C, the front wing on the other side raised, with the hind margins of the front wings in a straight line; D, the hind wing on one side raised; E, the hind wing on the other side raised; F, the antennae oriented and held in position by pins; G, removing the pin from the body of the butterfly.

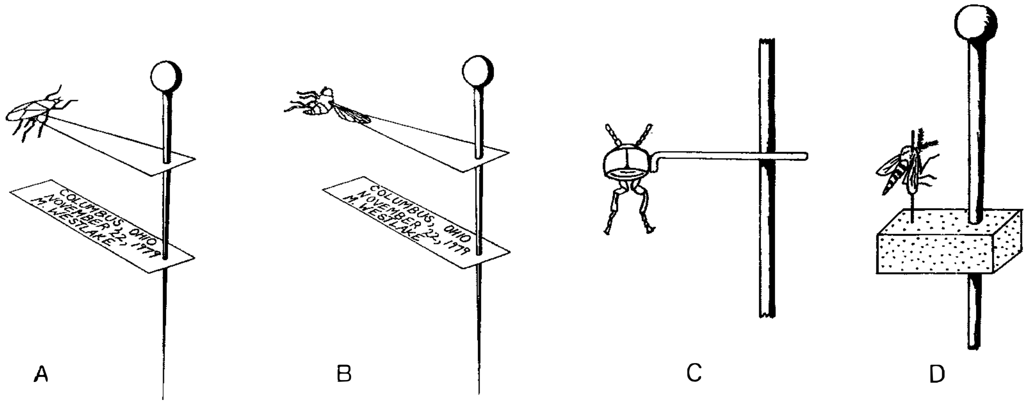


Figure 35–13 Methods of mounting minute insects. A, a bug on a point, dorsal side up; B, a fly on a point, left side up; C, a beetle mounted dorsal side up, attached by its side to the bent-down tip of the point; D, a mosquito mounted on a minuten pin.

factors as temperature and humidity. No general statement of time required can be made; you learn this by experience. To determine whether the specimen is ready to be removed from the spreading board, touch the abdomen gently with a pin: If the abdomen can be moved independently of the wings, the specimen is not yet dry; if the body is stiff, the specimen can be removed. Some of the larger moths may take a week or more to dry thoroughly. In every case, take care that not to lose the data on the specimen. A data label can be pinned alongside the specimen when it is spread.

In camp work or in the lower school grades, for example, mounting in a Riker mount or similar display is preferable to spreading a pinned specimen. Such specimens are more easily displayed and are less subject to breakage. However, spread specimens in good scientific collections are always pinned. Circumstances determine what type of spreading method to use.

Mounting Small Insects

Insects too small to pin can be mounted on a card or point (Figures 35–13A--C, 35–14), on a minuten pin (Figure 35–13D), on a microscope slide, or they can be preserved in liquid. Most small specimens are mounted on points.

Points are elongated, triangular pieces of light cardboard or heavy paper, about 8 or 10 mm long and 3 or 4 mm wide at the base. Remember that a well-prepared insect collection can last for centuries. Many types of paper do not have such longevity, becoming yellow and brittle in only a few short years. Therefore, points should be made of good-quality, acid-free, archival paper. The point is pinned through the base, and the insect is glued to the tip of the point. Points can be cut with scissors or, preferably, they can be cut with a special type of punch (obtainable from supply houses).

Putting an insect on a point is a very simple process. The point is put on the pin, the pin is grasped by the sharp end, and the upper side of the tip of the point is touched to the glue and then touched to the insect. Use as little glue as possible (so that body parts are not covered by it), and the specimen should be correctly oriented on the point. The standard positions of an insect mounted on a point are shown in Figure 35–13A–C.

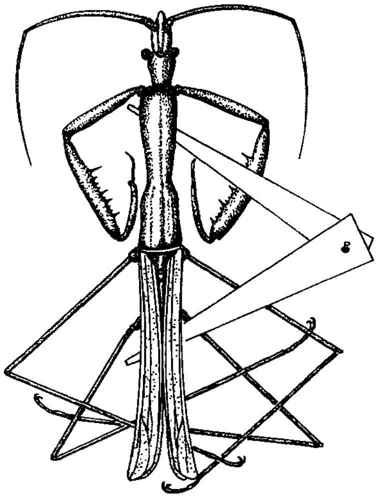


Figure 35–14 A method of mounting long, slender insects that are too small to pin; such insects are mounted on two points.

If the insect is put on the point dorsal side up (A), the point should not extend beyond the middle of the body. It is important not to embed in glue body parts to be examined for identification. Beetles mounted on points should always have the ventral side of the body visible.

The glue used in mounting insects on points should be quick-drying and should be quite hard when it sets. Preferably, it should be soluble in water or alcohol so that specimens can be easily removed if necessary (for example, for dissection or slide mounting.) Glue, used with care, is also useful in repairing broken specimens and replacing broken-off wings and legs. Shellac gel is a good glue for points. It can be purchased from a supply house or made following the instructions in Martin (1977).

Drying Specimens

Small specimens dry quickly in open air, but sometimes you may want to hasten the drying of larger insects artificially. Large specimens eventually dry in the open air, but it is not advisable to leave them exposed for very long because of the probability of damage by dermestids, ants, or other pests. A chamber with one or more light bulbs can be used for rapid drying. A simple drying chamber can be made from a wooden box with a door on one side. Slats can be placed on the sides of the box to allow mounting or spreading boards to be arranged at various distances from the heat source (the light bulbs). To allow moisture to escape, vent such boxes with a few small holes in the side or top.

Many soft-bodied arthropods (insect larvae, spiders, and others) can be dehydrated by critical-point drying, freeze-drying, vacuum drying, or chemical drying. These techniques yield specimens that are not particularly fragile, show no distortion and very little color loss, and subsequently show no indication of reabsorption of water or decomposition. After dehydration they are pinned and stored like any other pinned insect. The equipment and procedures used in critical-point drying are discussed by Gordh and Hall (1979), freeze-drying methods are described by Woodring and Blum (1963) and by Roe and Clifford (1976), and those for vacuum drying are described by Blum and Woodring (1963).

A recently developed method for chemical drying that has become popular is to use HMDS (hexamethyldisilazane). This highly caustic chemical should be used only in laboratories equipped with proper ventilation, preferably a fume hood. The method is generally as follows: (1) Specimens are dehydrated by passing them through higher and higher alcohol concentrations. Typically, a sample in 70% ethanol is transferred to a 95% solution for at least two hours; the sample is then transferred to a fresh solution of 95% ethanol. After two hours, the specimens are transferred to absolute alcohol for at least two hours, followed by transfer to a fresh vial of 100% ethanol. After the final two hours in the absolute alcohol, the liquid is removed as completely as possible and replaced with HMDS. After 20 minutes, the HMDS is removed and replaced with fresh HMDS. Finally the specimens are placed on filter paper and, with good ventilation, preferably in a hood, are allowed to air-dry. The times quoted vary widely depending on the nature of the specimens, the amount of water in the initial sample, and the quality of the chemicals used. Experiment to find the timing that works best for your material.

Preserving Insects in Fluids

Any type of insect can be preserved in fluid. Insects can be preserved in fluid temporarily until one has an opportunity to pin them, and many collectors prefer to store their collections in fluid rather than dried in envelopes or pillboxes. However, specimens preserved in fluids are usually not as easily examined as those on pins or points, and in general any insect that *can* be preserved dry should be mounted on a pin or point.

Preservation in fluids is the standard means of preservation for the following: (1) soft-bodied insects (for example, mayflies, caddisflies, stoneflies, midges, and others), which would shrivel and become distorted if pinned and allowed to air-dry; (2) many very small insects, which are best studied in detail when mounted on a microscope slide (for example, lice, fleas, thrips, Collembola, and others; (3) insect larvae and most insect nymphs; and (4) arthropods other than insects.

The fluid generally used for preserving insects and other arthropods is ethyl alcohol (70–80%). The preservation or fixation of tissues is better for many forms if certain other substances are added to the alcohol. The most commonly used modifications of ethyl alcohol are the following:

Hood's solution:

70–80% ethyl alcohol	95 ml
Glycerin	5 ml

Kahle's solution:

95% ethyl alcohol	30 ml
Formaldehyde	12 ml
Glacial acetic acid	4 ml
Water	60 ml

Alcoholic Bouin's solution:

80% ethyl alcohol	150 ml
Formaldehyde	60 ml
Glacial acetic acid	15 ml
Picric acid	1 g

Although these solutions are "classically" used, we must stress the dangers associated with some of the chemicals, particularly formaldehyde (a carcinogen) and picric acid (which is explosive when dry).

Ethyl alcohol (and the modifications just mentioned) can also be used as a killing agent for many insects and other arthropods, but it is unsatisfactory as a killing agent for insect larvae. The killing agents commonly used for larvae are the following:

KAAD mixture:	
95% ethyl alcohol	70–100 mL
Kerosene	10 mL
Glacial acetic acid	20 mL
Dioxane	10 mL

XA mixture:	
95% ethyl alcohol	50 mL
Xylene	50 mL

If KAAD is used, reduce the amount of kerosene for soft-bodied larvae such as maggots. Larvae killed in either of these mixtures are ready for transfer to alcohol for storage after ½ to 4 hours. In the transfer to alcohol, change the alcohol after the first few days, because it becomes diluted by the body fluids of the animal put in it. Any of these killing agents are likely to remove the bright colors of larvae, especially greens, yellows, and reds. All known killing and preserving fluids are likely to destroy some colors.

A problem always encountered when specimens are preserved in fluids is the evaporation of the fluid. Stopper the vials with rubber, neoprene, or polyethylene (not cork), and it is advisable to use oversized stoppers that do not extend very far into the bottle. Screw-cap vials are satisfactory if the cap is tight-fitting. Polyseal caps or inserts are very effective in reducing evaporation from screw-cap vials. Procaine vials or tubes (usually available free from any dentist) make ideal temporary containers for many small forms. All containers should be well filled with fluid and should be examined at least once or twice a year so that evaporated fluid can be replaced. Evaporation may be retarded by covering the stoppers with some sort of sealing material such as Parafilm. Another method is to place a number of small, stoppered vials in a large jar with a rubber gasket.

Mounting on Microscope Slides

Many small arthropods (lice, fleas, thrips, midges, mites, and others), and often such isolated body parts as legs or genitalia, are best studied when mounted on microscope slides. Material so mounted is generally transferred to a slide from preserving fluid, and the mount may be either temporary or permanent. Use temporary mounts for material that is to be returned to the preserving fluid after study. Such mounts may last anywhere from a few minutes to many months, depending on the mounting medium used. Use permanent mounts for material that is *not* to be returned to the preserving fluid after study. Despite their name, such mounts do not last indefinitely, but may remain in good condition for many years. Specimens mounted on microscope slides for class use are usually mounted as permanent mounts. Specimens of particular taxonomic value, which one would like to keep indefinitely, should be kept in fluids and mounted for study only in temporary mounts.

Many small or soft-bodied specimens may be mounted directly in a mounting medium, but others (especially dark-colored or thick-bodied specimens or such structures as genitalia) must be "cleared" before mounting. The clearing process removes tissue from within the specimen as well as some of the pigment. Generally it does not render a specimen truly clear or transparent. Some mounting media have an inherent clearing action. Several substances may be used specifically as clearing agents, but the most commonly used are probably potassium hydroxide (KOH), lactic acid, and Nesbitt's solution. KOH can be used for almost any arthropod or arthropod structure. Nesbitt's solution is often used for clearing such small arthropods as mites, lice, and Collembola. After clearing in KOH, wash the specimen in water (preferably with a little acetic acid added) to remove or neutralize any excess KOH. Specimens in lactic acid should be thoroughly washed with water. The subsequent treatment of the specimen depends on the type of medium in which it is mounted. Specimens cleared in Nesbitt's solution can be transferred directly to some mounting media, but with other media specimens must be run through certain reagents first.

KOH used for clearing is a 10–15% solution. The formula for Nesbitt's solution is as follows:

Nesbitt's solution:	
Chloral hydrate	40 g
Concentrated HCl	2.5 mL
Distilled water (more for lightly sclerotized specimens)	25–50 mL

Note that chloral hydrate is a controlled substance and is available only for restricted use.

KOH can be used cold or warm, or the specimen may be boiled in it. Boiling is faster but may sometimes distort the specimen. Clearing in cold KOH requires from several hours to a day or more. The same specimen may be cleared in a few minutes by boiling. Nesbitt's solution is usually used cold, and the clearing may require from a few hours to a few days.

Small specimens may be mounted on a regular microscope slide without any special support for the glass coverslip other than the mounting medium itself. Larger or thicker specimens should be mounted on a depression slide or with some sort of support for the cover glass, to keep it level and to prevent the specimen from being flattened. The support for a cover glass on an ordinary microscope slide may consist of small pieces of glass or a piece of fine wire bent into a loop. Some specimens are best studied in a depression slide or a small dish without a cover glass so that the specimen can be maneuvered and examined from different angles. If a cover glass is added, most specimens are mounted dorsal side up. Fleas are usually mounted with the left side up, and many mites are commonly mounted ventral side up.

The media most often used for temporary slide mounts are water or alcohol, glycerin, and glycerin jelly. Water and alcohol evaporate rapidly, and mounts with these materials generally last only a few minutes unless more of the medium is added. Temporary slides made with glycerin or glycerin jelly are much better and last a relatively long time. They can be made semipermanent by "ringing" (putting a ring of asphaltum, nail polish, or a similar material around the edge of the cover glass). With glycerin jelly, a bit of the jelly is put on the slide and liquefied by heat. Then the specimen is added and oriented, and a cover glass is put on. This material cools to a solid jelly. Specimens mounted in glycerin jelly can be unmounted by reversing the process. Specimens can be put into glycerin or glycerin jelly directly from water or alcohol.

The media used for permanent slide mounts are of two general types: those with a water base, and resins. Specimens can be mounted in water-based media directly from water or alcohol. Such mounts are somewhat less permanent than resin mounts, but their life can be prolonged by ringing. Specimens mounted in a resin (natural or synthetic) must first be dehydrated (by running through successively increasing concentrations of alcohol: for example, 70, 95, and 100%), and then through xylol and into the resin. The most commonly used resin is Canada balsam. There are many water-based media, but the following is one of the best:

Hoyer's chloral hydrate (Berlese's fluid):

Water	50 mL
Gum arabic	30 g
Chloral hydrate (see earlier comments)	200 g
Glycerin	20 mL

The gum arabic should be ground-up crystals or powder, not flakes. Filter this mixture through glass wool before use.

All permanent slide mounts take some time to dry. They should be kept horizontal (cover glass up) during drying and are best stored in slide boxes in this same position.

It is sometimes desirable to stain an insect before it is mounted. A number of different stains are suitable for this purpose; one very commonly used is acid fuchsin. The procedure to follow in using this stain on scale insects is outlined in Chapter 22.

Studies of Insect Genitalia

Many taxonomic studies of insects involve a detailed study of the external genitalia, particularly those of the male. The genitalia are sclerotized structures that can sometimes be studied in the dried insect without any special treatment of the specimen, but in most cases they are partly or largely internal and must be removed and cleared for detailed study.

Procedures to follow in removing and clearing genitalia vary depending on the type of insect. In some cases the insect (if mounted dry) can be relaxed, either by the use of a relaxing fluid (see earlier discussion) or by placing the specimen in a relaxing chamber for a time, and genitalia may be removed with a small dissecting needle and then cleared in KOH. In other cases the abdomen (or the apical part of it) must be removed and cleared in KOH, and the genitalia are dissected out after clearing. Clearing may be accomplished in a few minutes by boiling, or it may be accomplished by leaving the genitalia in the KOH for a longer period at room temperature. In the latter case, clearing may require from a few hours to a few days, depending on how heavily sclerotized these structures are. Lactic acid is generally more gentle as a clearing agent than KOH. Overclearing renders the genitalia transparent, fragile, and difficult to study. Such genitalia are more easily studied if stained with borax carmine after clearing.

After the genitalia are cleared, they are washed in water with a little acetic acid added (about 1 drop per 50 cm^3 of water) and placed in small dishes of glycerin for study. They can be mounted on microscope slides, but this approach permits a study from only one angle. In small dishes they can be turned and studied from any angle desired.

After the study is completed, the genitalia are stored in microvials of glycerin (vials about 10–12 mm in length), and these vials are kept with the specimens from which the genitalia were removed. If the genitalia came from a pinned specimen, the vial is put on the pin (the pin going through the stopper of the vial) below the specimen. Genitalia removed from a specimen must be handled in such a way that they can always be associated with the specimen from which they came as well as its collecting data.

Labeling

The scientific value of an insect specimen depends to a large extent on the information regarding the date and locality of its capture and also on such additional information as the name of the collector and the habitat

31°22.8'N 110°21.8'W
USA, Arizona, Cochise Co.
Bear Ck. Huachuca Mts.
18.iv.1994 N.F. Johnson
sweeping

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sweeping

Figure 35–15 Example of a word-processed document for collecting labels. The labels are set in 4-point type.

or food plant in or on which the specimen was collected. The beginning student may look on such labeling as an unnecessary and tedious chore, but the time always comes when data on a specimen are indispensable. An insect collector should *always* label his or her specimens with place and date as the minimum amount of data for a specimen. Additional data are desirable, but optional.

The label should follow this format and order: geographic coordinates, collecting locality, date(s) of collection, name of collector, collecting method, habitat or behavioral notes. For example, see Figure 35–15. The place of collection is by far the most important information on this label.

The geographic data are, admittedly, redundant, but specifying both the coordinates as well as indicating where the locality is, politically, makes the label easier to read and use. The coordinates are recorded to a 10th of a minute of latitude and longitude. As discussed earlier, the accuracy recorded and actually achieved varies for many reasons. A 10th of a minute is, roughly, 100–200 m, and is a reasonable level for most purposes. Some prefer to record UTM coordinates rather than lat/long. UTM, Universal Transverse Mercator, is a projection, that is, an algorithm for representing the Earth in the two dimensions of a map. The units reported are meters, which, together with a pair of base numbers—the false northing and false easting—uniquely indicate the position of a point on the planet. In some ways it is more convenient than degrees/minutes/seconds, because the units of latitude and longitude are equal. The surface of the Earth is divided into a number of zones to minimize distortions in the projection process. Converting UTM to lat/long requires that you know in which zone the coordinates occur. Any capable GPS unit can easily switch between recording coordinates in degrees/minutes/seconds, decimal degrees, or UTM.

The specification of collecting locality begins from a general level, the country, and becomes increasingly more specific. It has been traditional, in North America, that the country is not listed and the label begin with the state or province in which the specimen was collected. Including the country adds little to the amount of text on the label and certainly helps prevent any future ambiguity. Specification of the collecting locality should use a place name that other people can reasonably be expected to find and use, and may include an offset, such as "7 km S of West Bloomfield on SR56."

Traps are commonly operated for more than one day, and the date the traps were set and the date emptied is indicated by the range in days. Conventions for writing dates vary widely, and data recorded as, for example, 4/8/35 may mean April 8, 1935, to one person, but 4 August 1935, to another. This problem can be easily avoided by using roman numerals to represent the month of the year: 4.viii.1935. We also recommend that the year be specified using four digits.

The name of the collector is, arguably, the least important datum on a label. In some cases, however, it may be very helpful from a historical point of view or to enable you to go back to the collector for more information. On occasion you will find labels with either the abbreviation "coll." or "leg."—meaning collector or donor respectively.

Supplementary information commonly includes the method by which the specimens were collected, for example, swept, Malaise; the general habitat, such as "dry stream bed"; or behavioral notes such as "feeding on goldenrod flowers." Specimens that are reared from plant material, other arthropods, and those collected from a vertebrate host commonly have the abbreviation "ex: ..." to indicate that the specimen came "from" that host. Although useful, it is usually better to give more specific information, such as "reared from mature larva of *Papilio* sp."

Data labels can be printed by hand with a fine-pointed pen, but it is more effective to print them with a laser or ink-jet printer. The printer quality affects the quality, particularly longevity, of the labels produced. In general, labels produced with a laser printer should not be exposed to ethyl acetate. Four-point type is generally a good compromise between making the label small and keeping it legible. When large numbers of identical labels are needed, as is common when sweeping or using a trap, using the copy and paste functions of a word processor ensures that all the labels are identical. Generally, print no more than 6 lines of data on a single label. If more space is needed, use a second label rather than making a wide or long label. If the label is hand-written, use indelible ink.

The appearance of a collection of pinned insects is greatly influenced by the nature of the labels. Small, neat, properly oriented labels add much to the aesthetic value of the collection. Labels should be on fairly

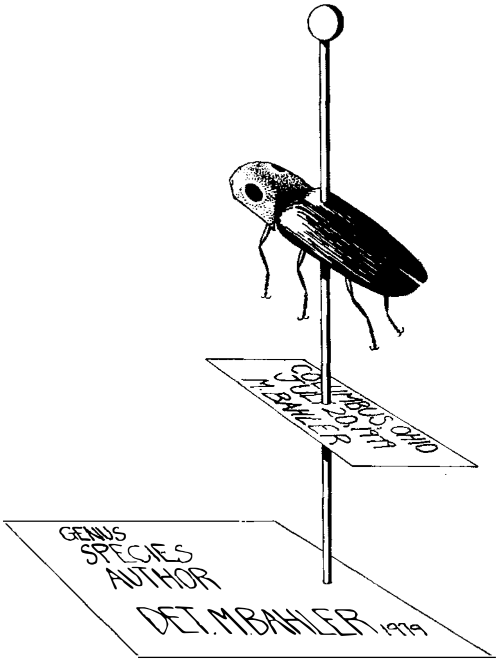

Figure 35–16 The identification label, giving the scientific name of the insect and the name of the person identifying the specimen.

stiff white paper and preferably not larger than 6 by 19 mm. The paper should be good quality and acid-free. Place labels at a uniform height on the pin, parallel to and underneath the insect. If only one label is used, place it about 16 mm above the point of the pin. If more than one label is used, the uppermost one should be at this distance above the point. Orient the labels so that all read from the same side. We prefer that they read from the left side (Figure 35–16), but some people prefer that they read from the right side. For specimens mounted on points, the label should extend parallel to the point (Figure 35–13A,B) and be offset from the pin like the point. If there are two or more labels on the pin (for example, one for the locality, date, and collector, and another for the host plant), the labels should be parallel and arranged to be read from the same side.

This discussion applies to labels containing data concerning the locality, date, and collector, and not to labels identifying the insects. Identifying labels are discussed next, under "Housing, Arrangement, and Care of the Collection."

Labels for specimens preserved in fluids should be written on a good grade of rag paper with India or other waterproof ink, or printed as just described, and placed inside the container with the specimen(s). Labels for specimens mounted on microscope slides are attached to the upper surface of the slide, on one or both sides of the cover glass.

Housing, Arranging, and Caring for the Collection

The basic considerations in housing, arranging, and caring for an insect collection are the same whether the collection consists of a few boxes of specimens or thousands of museum drawers containing millions of specimens. The specimens in a collection must be systematically arranged and protected from museum pests, light, and moisture. The general arrangement of a collection depends principally on its size, the purpose for which it is intended, and the method used in preserving the specimens (pinned, in envelopes, in liquid, on slides, and so on).

Keep pinned insects in dust-proof boxes having a soft bottom that will permit easy pinning. Several types of insect boxes may be purchased from supply houses. The most commonly used type is made of wood, about 230 by 330 by 60 mm in size, with a tight-fitting lid and an inner bottom of sheet cork, composition board, or foam plastic. Such boxes usually cost from $10 to $25. The better boxes of this type are called Schmitt boxes. Satisfactory low-cost pinning boxes can be made of cigar boxes or heavy cardboard boxes by lining the bottoms with sheet cork, balsa wood, foam plastic, or soft corrugated cardboard. This bottom material should be glued in place or cut so that it fits very tightly into the box.

For a small collection housed in one or a few boxes, an arrangement similar to that shown in Figure 35–17 is suggested. It is unlikely that anyone except the specialist will have the specimens in his or her collection identified further than to family, and for many collectors, particularly a beginner, it may be difficult enough to carry the identification that far. The simplest arrangement, therefore, is to have the specimens arranged by order and family, with the order label (containing the order name and common name) on a separate pin and the family label (containing family and common names) either on a separate pin or on the pin of the first insect in a row of specimens in that family. There are various ways of arranging the specimens in a small collection, but the arrangement should be neat and systematic, and the labels should be easily seen.

Most large institutions and many private collectors house their collections in uniform glass-topped museum drawers that fit into steel cabinets. Specimens may be pinned directly into the cork or foam plastic bottoms in such drawers, but usually they are pinned

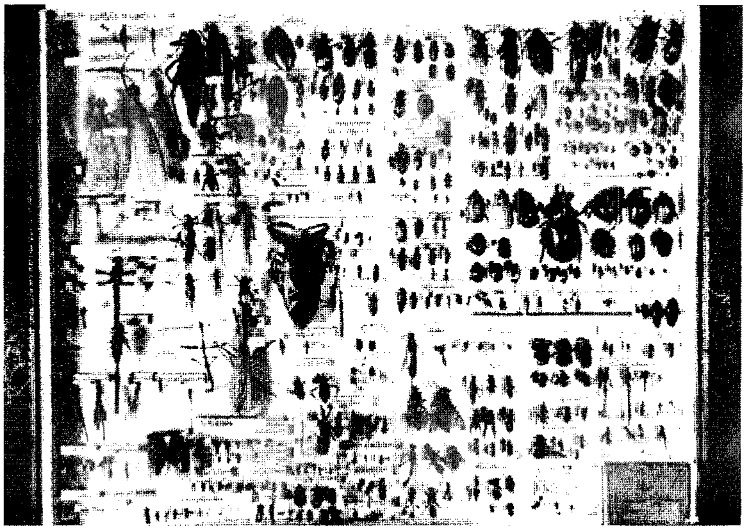

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Figure 35–17 A synoptic insect collection.

in small unit trays of various sizes that fit snugly in the drawers (Figure 35–18). The unit tray system facilitates rapid expansion and rearrangement of the collection without the need to handle individual specimens, which is time-consuming and hazardous to the specimens. The unit trays are of a convenient size to fit under a dissecting microscope, so that unless it is necessary to examine the ventral surface of a specimen, the specimen can be examined without being removed from the tray, thus reducing the chance of breakage.

In larger collections, such as those of specialists or those in museums, where the specimens are identified to species, the species determination is usually put on a plain white or bordered label placed low on the pin against the bottom of the box. This label contains the complete scientific name (genus, species, subspecies if any), the name of the describer, the name of the person making the determination, and the date (traditionally the year only) the determination was made (Figure 35–16). In large collections where each drawer contains a series of unit trays (Figure 35–18), each tray usually contains specimens of just one species.

Many insect collectors eventually become interested in and concentrate their efforts on a particular order, family, or genus. By contacts and exchanges with other collectors interested in that group, a collector may build up a sizable collection and be in a position to contribute to knowledge of that group through sci-

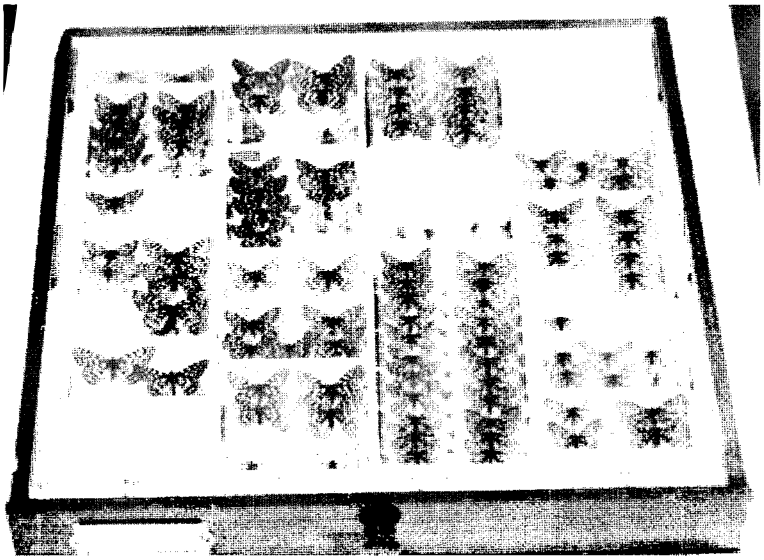

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Figure 35–18 A drawer of a large insect collection.

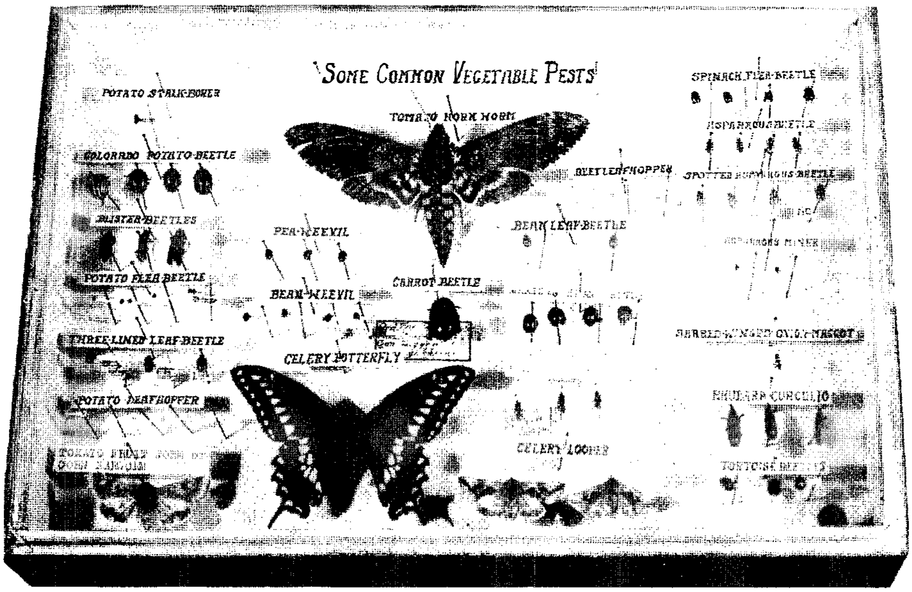

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Figure 35–19 An illustrative collection, showing some common pests of vegetables.

entific publication. Some collectors prefer to specialize on insects from a particular habitat (aquatic insects, wood borers, flower-frequenting insects, gall insects, leaf miners, and so on), medically important insects, insect pests of particular types of plants (Figure 35–19), beneficial insects, or those with particular habits (predators, parasites, scavengers, and so on). The possibilities are many.

We believe that everyone interested in entomology, regardless of the field in which he or she is primarily interested, should concentrate on a particular taxonomic group. A certain satisfaction comes with a thorough knowledge of even a small group of animals, and such study can prove to be very interesting for a person whose major interest or occupation is in another field.

Display Mounting

Many collectors may wish to keep their collection in containers where the insects can be easily displayed. Several types of mounts are useful for this purpose. A pinned collection can be easily displayed if it is mounted in glass-topped boxes or in glass-doored wall cabinets. In the latter case, cover the back of the cabinet with a material that will permit easy pinning. Butterflies, moths, and many other insects can be displayed in Riker mounts—boxes in which the insects are directly under the glass top, on cotton batting (Figure 35–20). Cases somewhat similar to Riker mounts, but without the cotton and with glass on the top and bottom (Figure 35–21A), are useful for displaying one or a few specimens (that is, one or a few in each mount). It is also possible to enclose specimens between sheets of plastic or to embed specimens in plastic.

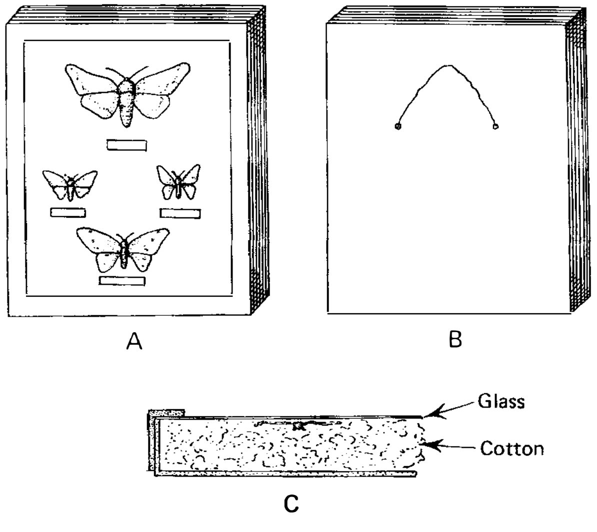

Figure 35–20 Riker mount. A, front view; B, back view; C, sectional view showing a specimen in place under glass on cotton.

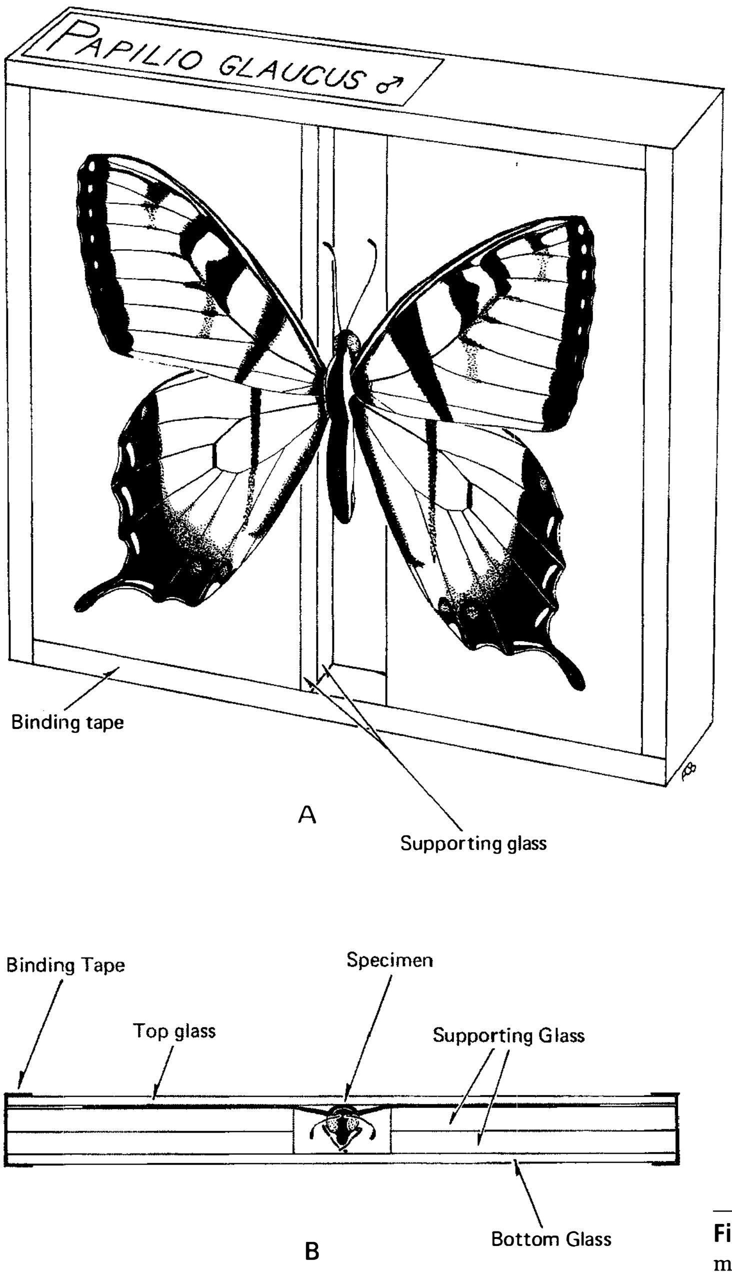

Figure 35–21 All-glass mount. A, completed mount; B, sectional view of mount.

A Riker mount (Figure 35–20) is a cotton-filled cardboard box with most of the lid removed and replaced with glass, and with the glass top holding the insects in place on the cotton. Riker mounts may be of almost any size (0.3 by 0.4 m is about the largest size that is practical) and are about 19 to 25 mm deep. They can be bought from supply houses. When placing large-bodied insects in a Riker mount, tease a little hole in the cotton with forceps for the insect body. After the specimens are in the box, put the lid is back on and fasten it with pins or tape.

Glass mounts are similar to Riker mounts, but without the cotton and with glass on the top and bottom (Figure 35–21). They are excellent for displaying individual moths, butterflies, or other insects.

Protecting the Collection

All insect collections are subject to attack by dermestid beetles, ants, and other museum pests, and if the collection is to last any length of time, certain precautions must be taken to protect it from these pests. Various materials may be used for this purpose, but one material commonly used is naphthalene (in flake or ball form). Naphthalene flakes can be put into a small cardboard pillbox that is firmly attached to the bottom of the insect box (usually in one corner) and has a few pin holes in it. Paradichlorobenzene (PDB) can also be used, but it volatilizes more rapidly than naphthalene and must be renewed at more frequent intervals. Also, health concerns are associated with long-term exposure to a chlorinated hydrocarbon such as PDB. To protect specimens in Riker mounts, sprinkle naphthalene flakes under the cotton when making the mount. Check a collection periodically to make sure that plenty of repellent is present. If boxes or drawers are stored in tight cabinets that are not opened frequently, the repellent should last a long time.

Note that paradichlorobenzene and naphthalene are only repellents, and although they will keep out potential pests, they will not kill pests already in the collection. If you find a box or drawer infested with pests, fumigate it to destroy these pests. Heating boxes, cases, or mounts to 150°F (66°C) or higher for several hours (if the boxes are such that the heat will not damage them) will destroy any dermestids or other pests they may contain. Similarly, rapidly reducing the temperature to −30°F (−35°C) and holding the specimens at that temperature for several days is also effective, although slower. Because of concerns about long-term human exposure to chemicals, many large institutional collections are moving toward freezing as a means of sanitation. Many good collections have been ruined by pests because the collector failed to protect them.

Packing and Shipping Insects

A dried insect on a pin is such a fragile object that it would seem almost impossible to ship a box of pinned insects through the mail and have it arrive at its destination with the specimens intact. But it can be done if a few simple rules are followed. The preparation of specimens for shipment largely depends on the treatment they are likely to receive in transit: They will be turned upside down and sideways and subjected to severe and repeated jarring. Therefore, the two most important considerations are to make certain that all pins are firmly anchored, so that they cannot work loose and bounce around and break specimens, and that the box in which they are pinned is placed in a larger box, surrounded by packing material to cushion the blows the package will invariably receive.

Note that we are concerned here with the transporting or shipping of *dead* insects. Before transporting or shipping living insects, check with quarantine officials and the postal authorities.

Insert pinned specimens firmly into the bottom of the insect box, preferably with pinning forceps. The bottom of the box should be of a material that will hold the pins firmly. Brace large specimens with extra pins to prevent them from swinging around and damaging other specimens. Use extra pins to brace and support long appendages, or a long abdomen. Place a sheet of cardboard cut to fit the inside of the box (with a slot cut out along one side to facilitate removal) over the top of the pinned specimens, and fill the space between this and the lid of the box with cotton batting, Cellucotton, a plastic bubble sheet, or a similar material. This arrangement keeps the pins from being dislodged during shipment. *Never* include vials of insects in a box of pinned specimens, regardless of how firmly the vials may seem to be fastened in the box. The rough handling the average box gets when in transit may dislodge even the most "firmly" attached vial and destroy the specimens.

If a box of pinned insects contains specimens from which the genitalia (or other parts) have been removed and stored in a microvial on the pin below the insect, take special precautions to make sure these vials do not come loose and damage specimens in the box. Insert pins containing such vials far enough so that the vial rests on the bottom of the box. The vial is then held in a fixed position by insect pins, one placed at the end of the vial and two other crossed over the middle of the vial.

When shipping specimens preserved in fluids, take measures to protect the specimens in the containers. The containers should be completely filled with fluid, and it is sometimes desirable to add cotton or some similar material in the container to keep the specimen from bouncing about. Small and delicate larvae, such as mosquito larvae, should be in vials so completely filled with fluid that there is not even an air bubble in the vial. An air bubble in a vial can have the same effect on a specimen as a solid object in the vial would have. One method of removing all air bubbles is to use glass tubes stoppered with rubber stoppers, filling the vial containing the specimens to the brim and then carefully inserting the stopper with a pin alongside it (to allow excess fluid to escape). When the stopper is in place, remove the pin.

If two or more containers of insects in fluid are packed in the same box, wrap them in wide strips of Cellucotton, bubble wrap, or some similar soft material so that no two vials are in contact. The most common preservative fluids contain either ethanol or isopropanol, both of which are classified as flammable liquids. A number of regulations govern the shipping of such liquids, either by the postal services or commercial courier services. At the time of this writing, alcohol cannot be sent in international mail or by domestic airmail. Alcohol may be sent within the United States by surface mail as long as packaging and mailing requirements are met. You should contact private companies for their own regulations.

Insects in glass or Riker mounts can ordinarily withstand considerable jolting without damage, but take care that the glass of these mounts does not get broken. Pack such mounts in an abundance of soft packing material, and make sure no two of them touch each other in the box.

Insect material mounted on microscope slides should be shipped in wooden, plastic, or heavy cardboard slide boxes, preferably boxes in which the slides are inserted into grooves and are on edge in the box. Place strips of a soft material between the slides and the lid of the box, so that the slides do not bounce about.

Dried specimens in envelopes or pillboxes should be packed in such a way that the specimens do not bounce around inside the box. Pad pillboxes inside with Cellucotton to immobilize the specimens, and fill boxes containing envelopes with cotton or Cellucotton.

Boxes containing pinned insects, insects in fluids, microscope slides, or dried insects in envelopes or pillboxes that are to be sent through the mail should be wrapped in paper, to keep out fragments of packing material, and packed inside a larger box. Choose the outer box so as to allow at least 50 mm of packing material (excelsior, shredded paper, cotton, Styrofoam chips, and so forth) on all sides of the smaller box. This packing material should not be so loose as to allow the inner box to rattle around or so tight that the cushion effect is lost.

Whenever material is shipped through the mail, send an accompanying letter to the addressee, notifying him or her of the shipment, and include a copy of the letter in the package. Packages of dead insects sent through the mail are usually marked "Dried (or Preserved) Insects for Scientific Study." It is well to mark such packages for gentle handling in transit, although such marking does not always ensure that they will not get rough treatment. Material shipped to points inside the United States should be insured, though it may be difficult to place an evaluation on some material. The statement "No Commercial Value" on a box shipped from one country to another will facilitate the box getting through customs.

Work with Living Insects

Anyone studying insects who does nothing but collect, kill, and mount these animals and study the dead specimens will miss the most interesting part of insect study. The student who takes time to study *living* insects will find that they are fascinating and often amazing little animals. Living insects can be studied in the field or in captivity. Many are very easy to keep in captivity, where they can be studied more easily, and often at closer range, than in the field.

Keeping Living Insects in Captivity

Relatively little equipment or attention is required to keep an insect alive in captivity for a short period. Insects can be brought in from the field, kept in a cage of some sort for a day or so, and then released. Rearing adult insects from their immature stages or maintaining cultures of insects through one or more generations usually requires more equipment and attention. However, many types of insects are fairly easy to rear or culture.

Rearing adult insects from immature stages is an excellent way to learn about their habits and life histories. The activities of insects in cages can generally be more easily observed, and certainly observed to a greater extent, than insects in the field. Many insects collected as immatures and reared will be found to have been parasitized, and the parasites will emerge rather than the host insect, particularly in the case of caterpillars.

Cages for Insects. Almost anything can serve as a suitable cage for keeping insects in captivity for a short time or for rearing some types of insects. The simplest type of cage is a glass (or clear plastic) jar of some sort covered with gauze held in place with a string or rubber band (Figure 35–22A). The jar may vary in size from a small vial up to a large (4-liter or larger) jar, depending on the size and numbers of the insects. In some cases food, water, or other materials necessary to the well-being of the insects can simply be placed in the bottom of the jar. Such containers are also suitable for aquaria. Mosquitoes, for example, can be reared in vials that hold only a few cubic centimeters of water.

Cages suitable for rearing some types of insects or for display can be made of cardboard, gauze, and clear plastic. Any small cardboard box can be used. Its size depends on the size of the insect it is to contain. Holes cut in the ends and covered with gauze provide ventilation; clear plastic or glass in the front provide visibility; and the top can be covered with glass, clear plastic, or an opaque lid.

A more permanent type of cage can be made of window screen with a wood or metal framework. The bottom 25 mm or so of a large metal can with a cylinder of screen inserted in it (Figure 35–23B) makes a good cage. Cages of wood and screen can be made with the opening at the top, like a lid, or with a door on one side. If the cage is to be used for fairly active insects and it is necessary to get into the cage frequently, provide it with a sleeve (Figure 35–23A).

When rearing a plant-feeding insect, and the plant on which it feeds is not too large, you can rear the in-

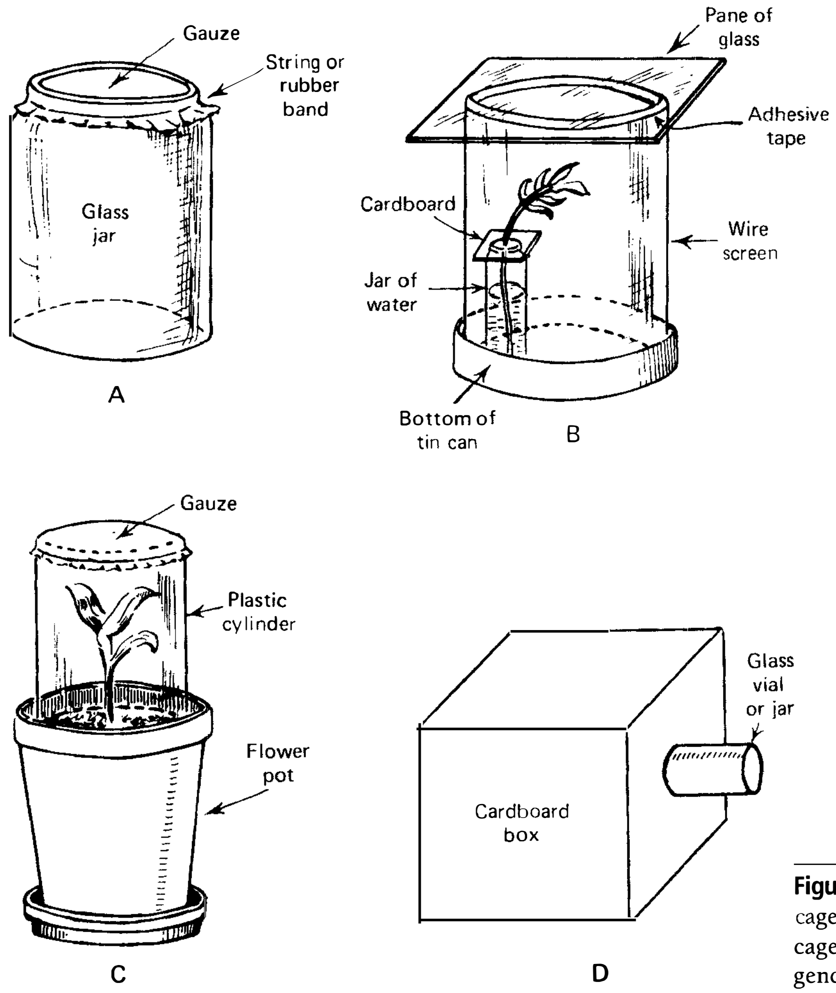

Figure 35–22 Some types of insect cages. A, jar cage; B, cylindrical screen cage; C, "flowerpot" cage; D, an emergence box.

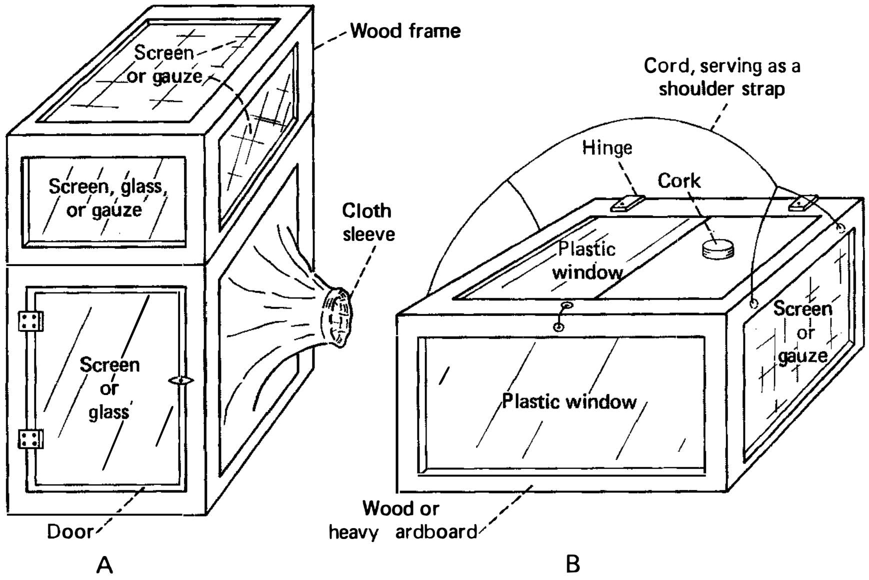

Figure 35–23 Insect cages. A, sleeve cage; B, a field carrying cage.

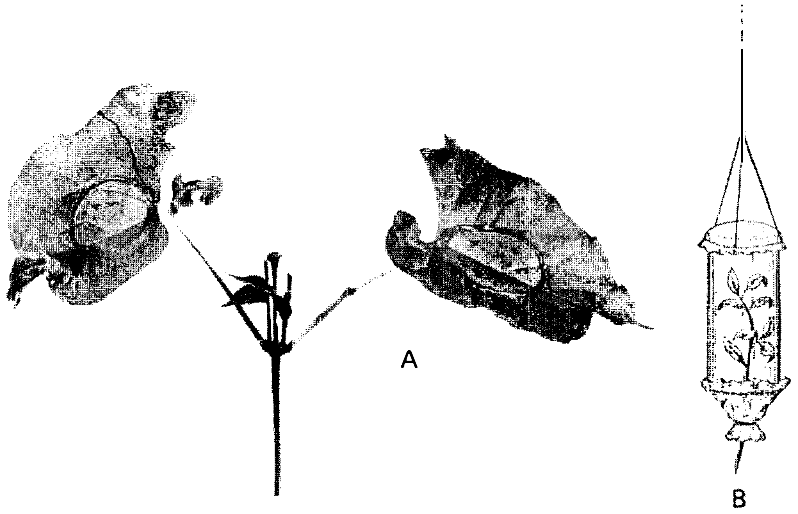

Figure 35–24 Methods of caging insects in the field. A, tanglefoot barrier on a leaf, for small nonflying insects; B, cage of plastic and gauze for caging insects on their food plant. (A, courtesy of Davidson.)

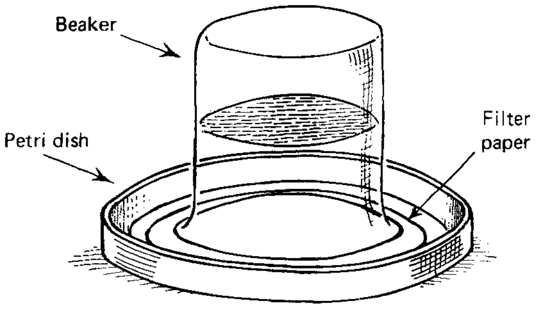

Figure 35–25 Method of providing water for caged insects.

sect in a "flowerpot" cage (Figure 35–22C). The plant is planted in a flowerpot or a large can, and a cylinder of glass, plastic, or screen is placed around the plant and covered at the top with gauze.

An emergence box such as shown in Figure 35–22D works well for rearing adults from larvae living in debris, soil, excrement, and other materials. The material containing the larvae is placed in the box, which is then closed tightly. When the adults emerge, they are attracted by the light coming into the box through the vial, and go into the vial.

The best way to rear some insects is to leave them in their habitat in the field and cage them there. Many types of cages can be constructed around an insect in the field. In the case of a plant-feeding insect, a cage consisting of a roll of clear plastic or fine screen, with gauze at each end, can be placed around that part of the plant containing the insect (Figure 35–24B), or a cage made of window screen on a wooden framework can be built about part of the plant. Many plant-feeding insects can be confined on a certain part of a plant by means of barriers of some sort, such as Tanglefoot bands (Figure 35–24A). Aquatic insects can be reared in cages of screen submerged in their habitat. The screen should be fine enough to prevent the escape of the insect but coarse enough to allow food material to enter.

Cages made of heavy cardboard or wood, gauze, and plastic can easily be fitted with a shoulder strap and used to bring living material from the field into the laboratory or classroom. With a carrying cage such as the one shown in Figure 35–23B, large materials can be put into the cage by lifting the lid, or single insects can be put into the box through the hole in the lid.

When rearing insects indoors, you must usually make sure that the conditions of temperature and humidity are satisfactory and must provide enough food and water. Many insects, such as leaf-eating caterpillars, must be regularly provided with fresh food. Add fresh leaves every day or so, or find some way to keep large amounts of foliage fresh in the cage for several days at a time. If the insect needs water, the water may be provided by means of a beaker inverted in a petri dish (Figure 35–25); by a vial full of water, plugged with cotton, and lying on its side in the cage; by a sponge soaked with water; or by some similar means.

Some Easily Reared Insects. Some of the easiest insects to rear indoors are those that normally live indoors, for example, the insects that attack flour, meal, or other stored food products. They can be kept and reared in the original container of the food material or in a glass jar covered with fine gauze. It is usually not necessary to provide these insects with moisture. The various stages of the insect can be obtained by sifting the meal, and some of these can be added to fresh meal to keep the culture going.

Cockroaches are excellent insects for rearing, because they are fairly large and active, most people are familiar with them, and in most places they are abundant and easily obtained. A culture can be started by trapping some adults. Cockroaches can be reared in various types of containers, a large glass or plastic jar covered with gauze, or even an open box, provided the box is several centimeters deep and the upper 50 or 75 mm of the sides is smeared with petroleum jelly so that the cockroaches cannot climb out. These insects are practically omnivorous, and many different types of material will serve as suitable food. Dog biscuits make a good food. Plenty of water should be provided.

Many types of insects that have aquatic immature stages can be reared easily from the immature to the adult stage. The type of aquarium needed depends on the type of insect being reared. Small forms feeding on organic debris or microorganisms can be reared in containers as small as vials. Larger ones, particularly predaceous forms, require larger containers. Larvae or pupae of mosquitoes, for example, can be kept in small containers in some of the same water in which they were found, with a cover over the container to prevent the escape of the adults. For vials, the simplest cover is a plug of cotton. In many cases it is necessary to simulate the insect's habitat in the aquarium (for example, have sand or mud in the bottom and have some aquatic plants present), and in the case of predaceous insects, such as dragonfly nymphs, smaller animals must be provided as food. The water must be aerated for some aquatic types. In maintaining an aquarium, try to keep all the conditions in the aquarium as close as possible to conditions in the animal's normal habitat.

When attempting to maintain aquatic insects in the laboratory generation after generation, make special provision for the different life-history stages that frequently require special food, space, or other conditions. Some mosquitoes are relatively easy to maintain in culture in the laboratory, especially species that normally breed continuously through the warmer parts of the year, and in which the adults do not require a large space for their mating flights. The yellow fever mosquito, *Aedes aegypti*, is easily cultured in the laboratory.[1] At a temperature of 30°C (85°F) the development from egg to adult requires only 9–11 days. The females must obtain a blood meal before they can produce eggs. A person's arm can provide this meal, but a laboratory animal such as a rabbit (with the hair shaved from a portion of its body) is better. Please note, though, that the U.S. government closely regulates the use and care of vertebrates in the laboratory. Adult mosquitoes are allowed to emerge in cages with a capacity of about 0.028 m^3 (1 ft^3). A solution of honey in the cage provides food for the males (which do not feed on blood) and for the females before their blood meal.

Place a small dish of water in the cage for egg laying. If paper or wooden blocks are placed in this water, the eggs are deposited on these at the margin of the water as it recedes. These eggs usually hatch within 10 to 20 minutes after they are placed in water at room temperature, even after months of desiccation. If the larvae are reared in large numbers, they are best reared in battery jars. As many as 250 larvae can be reared in a 150-mm battery jar half-filled with water. The larvae can be fed ground dog biscuit, which is sprinkled on the surface of the water daily. For the first-instar larvae, use 30–35 milligrams daily. Increase this amount for successive instars, up to 140–150 milligrams daily for fourth-instar larvae. Fourth-instar larvae pupate 7–9 days after the eggs hatch, and adults emerge about 24 hours later.

It is usually fairly easy to rear adult insects from galls. The important thing in rearing most gall insects is to keep the gall alive and fresh until the adults emerge. The plant containing the gall can be kept fresh by putting it in water, or the gall can be caged in the field. If the gall is not collected until the adults are nearly ready to emerge (as determined by opening a few), it can simply be placed inside a glass jar, in a vial of water, and the jar covered with gauze. This same procedure can be used to rear out adults of leaf miners that pupate in the leaf. If the leaf miner pupates in the soil (for example, certain sawflies), grow the plant containing the insect in a flowerpot cage.

Adults of some wood-boring insects are easily reared. If the insect bores into drying or dried wood, the wood containing the larvae can be placed in an emergence box like that shown in Figure 35–23D. If the insect bores only in living wood, the adults can be obtained by placing some sort of cage over the emergence holes (in the field).

Termite cultures are easily maintained in the laboratory and are of value in demonstrating the social behavior and the wood-eating and fungus-cultivating habits of these insects. Various types of containers can be used for termite culture, but the best for demonstration purposes is either a battery jar or a glass-plate type of container (Figure 35–26). A termite colony can last quite a while without queens in either type of container, but will prove more interesting if queens or supplemental queens are present.

If a battery jar is used, put 6 mm or so of earth in the bottom of the jar and place a sheet of wood on either side of the jar. Balsa wood is best because the termites become established in it quickly. Put thin, narrow strips of a harder wood on each side between the balsa wood and the glass, and put pieces between the

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[1] Because this species is an important disease vector, special precautions should be taken to prevent the escape of any individuals reared.

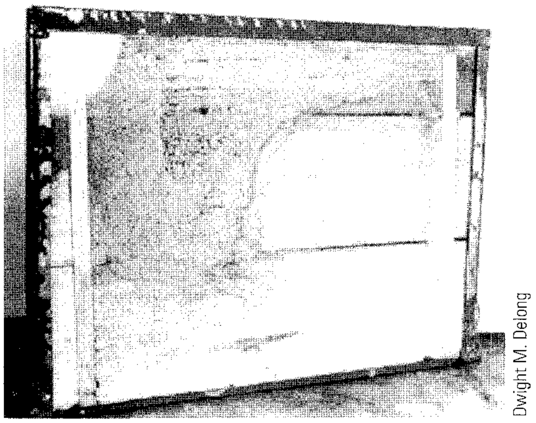

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Figure 35–26 Glass-plate type of container for rearing termites.

sheets of balsa wood to hold them in place. In such a container termites become established in a few hours. They tunnel through earth and wood and build fungus "gardens" (apparently an important source of nitrogen and vitamins) between the wood and the glass. The wood will be destroyed in a few weeks and must be replaced. Water must be added every few days: A pad of cotton can be thoroughly moistened and placed between the glass and the wood at the top of each side.

A glass-plate type of container is somewhat similar to the ant nest described later, but has a metal rather than a wood frame (Figure 35–26). The container should be about 0.3 m wide, 0.3 m high, and 13 mm thick, and should have a pan at the base to hold it upright. No earth need be used in this type of container. Place a piece of balsa wood in the container, with narrow strips inserted between it and the two glass plates (front and rear). Put the termites in the space between the wood and glass. Place a thin pad of cotton batting over the top of the wood, between the two glass plates, and thoroughly soak this with water about twice a week. The fungus gardens are maintained here as in the battery-jar culture.

The chief problem encountered in rearing caterpillars is providing suitable food. Because many caterpillars feed only on certain species of plants, you must know the food plant of a caterpillar you want to rear. Caterpillars can be reared in almost any sort of cage, provided the cage is cleaned and fresh food is provided regularly. Plant food stays fresh longer if put in a small jar of water inside the cage. A cover on the top of the water jar, around the stem of the plant, keeps the caterpillars from falling into the water (Figure 35–22B). Some caterpillars require special conditions for pupation. Butterfly larvae usually pupate on the leaves or on the sides or top of the cage. Most moth larvae pupate in the corner of the cage or under debris of some sort. Moth larvae that pupate in the ground (for example, the larvae of sphinx moths) should be reared in a cage containing several centimeters of soil.

Many of the larger moths pupate in the fall and emerge as adults in the spring, and their cocoons can be collected in the fall. If these cocoons are brought indoors in the fall, they may dry out or the adults may emerge in the middle of the winter (though the second possibility may not be objectionable). The drying can be prevented by putting the cocoons in a jar that has 25 mm or so of soil in the bottom and sprinkling the soil and cocoon with water about once a week. To keep the moths from emerging in the middle of winter, keep them in screen cages (preferably cages containing some dirt or debris) outdoors (for example, on the outside windowsill of a room). If an emerging moth kept in an outdoor cage is a female, and if it emerges at a time when other moths of its kind are on the wing, it will often attract male moths from a considerable distance.

Because of their social behavior, ants are very interesting animals to maintain in indoor cages. The simplest type of ant cage, particularly for display, is a narrow vertical cage with a wooden framework and glass sides (Figure 35–27). This is filled with an ant–soil mixture obtained by digging up an ant hill, preferably a small one under a stone or board. This mixture should contain all stages and castes if possible. The queen can usually be recognized by her larger size. The glass sides of the cage should be darkened by covering them with some opaque material; otherwise, all the tunnels the ants make will be away from the glass and not visible. Food and moisture must be provided. Food can be provided by putting a few insects into the cage from time to time or by putting a few drops of diluted molasses or honey on a small sponge or wad of cotton in the cage. Moisture can be provided by keeping a wet sponge or wad of cotton on the underside of the lid or on top of the dirt.

An observation beehive makes an excellent class demonstration. It can be set up inside an open window, and the bees can come and go at will, yet students can watch all that goes on inside the hive. Space here does not permit a detailed description of how to construct an observation beehive, but Figure 35–28 shows what it is like. If you want to set up an observation beehive, get in touch with a local beekeeper and ask for help and suggestions.

A number of insects prove interesting to rear or maintain for a short time in captivity. Singing insects such as crickets, katydids, or cicadas can be kept caged for a time with relatively little difficulty. If case-making insects are caged, it often possible to observe how the cases are made, and perhaps special materials (such as

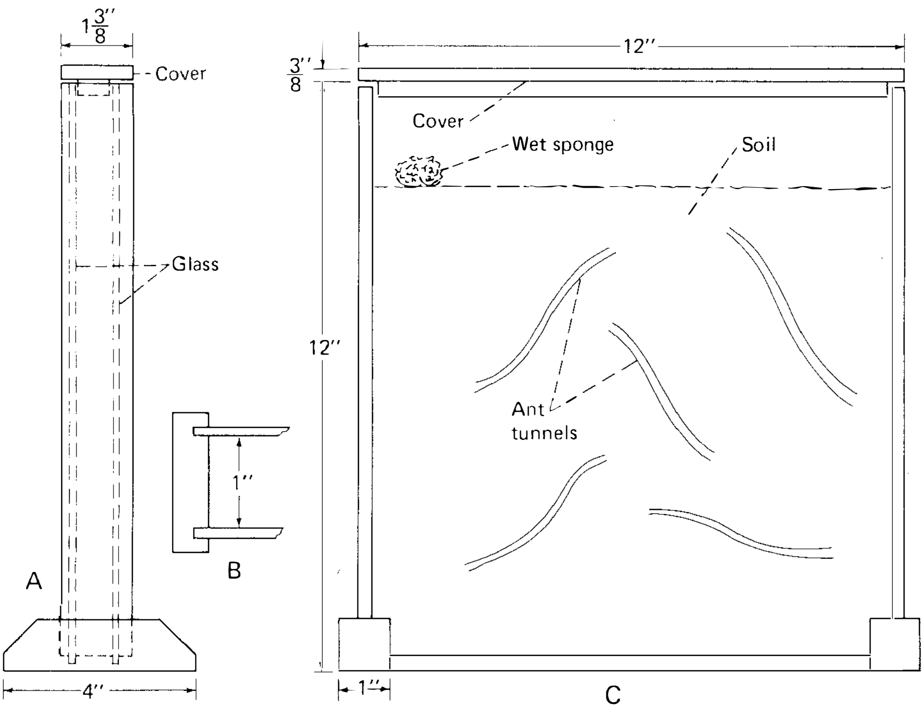

Figure 35–27 Vertical type of ant cage. A, end view; B, top view of one end showing cage construction; C, front view.

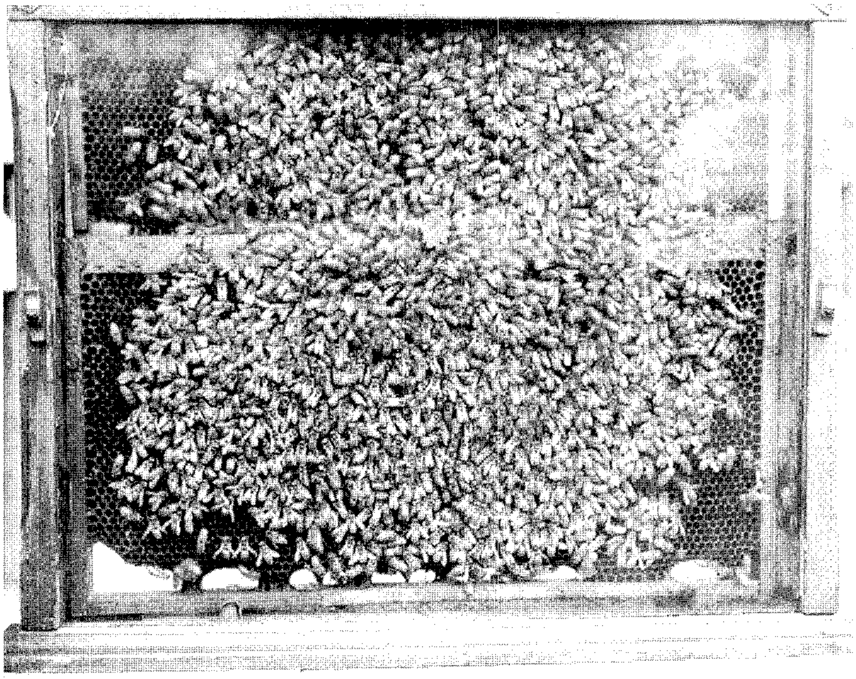

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Figure 35–28 Observation beehive.

colored bits of glass for caddisfly larvae usually using sand grains) can be provided for the case. Caging predaceous insects with their prey (particularly mantids), or parasitic insects with their hosts, can demonstrate these interrelationships. With a little knowledge of the food habits and habitat requirements of a species, the ingenious student can usually devise methods of rearing almost any type of insect.

Photographing Insects

Photographing insects, especially in color, has become a common practice of both the professional entomologist and the layperson. Insect photographs are used extensively to illustrate books, bulletins, or journal articles, for class use, and for illustrating public lectures. Many books have been written about the photography of insects and other natural history subjects, so we need not go into this subject in detail here.

A large assortment of lenses, filters, adapters, and synchronized flash and other lighting equipment is currently available, so that the photographer can select almost anything needed to photograph, either the entire insect or a small part of it. Lenses are available for almost any size of magnification desired.

Pictures of dead or mounted insects are useful for some purposes, but pictures of living insects, or at least insects that *look* alive and are in a natural pose, are far better. Taking such pictures is often difficult, but the problem can be solved in one of two general ways: (1) by using equipment that permits a very short exposure time, and getting as close as possible without disturbing the insect; and (2) by stupefying the insect temporarily so that more time is available for taking the photograph. Using various chemicals (for example, CO_2) or chilling the insect, can condition it for this type of photographic exposure. It is often possible to get a good picture by training the camera on a spot where the insect will eventually alight and then waiting for the insect to alight there. Many insects can be photographed by aiming the camera at a flower and photographing the insects when they come to the flower.

Photomicrographic equipment (camera, lighting, and so on) has been developed that can be attached to (or built into) a microscope. Such equipment enables one to photograph very minute insects, or parts of insects, at high magnification. The scanning electron microscope (SEM) is another piece of equipment that produces pictures of very high magnification, often showing details that cannot be seen with an ordinary microscope.

You can get pictures of considerable entomological interest without photographing any insects at all. Insect nests or cocoons, damaged leaves or other objects, wood-borer tunnels, and similar objects make excellent photographic material and are usually much easier to photograph than living insects.

Photographing insects has become a hobby with many naturalists and camera enthusiasts, who choose insects as well as flowers and birds because of their color patterns or because they are intrigued by the habits and biology of these animals.

Drawing Insects

A serious student will sooner or later have occasion to make drawings of insects or insect structures, either for personal notes, as a part of a laboratory exercise, or as part of a research report prepared for publication. You need not be a natural artist to prepare good drawings of insects. The first aim of entomological drawing is accuracy rather than artistry, and simple line drawings often serve better than elaborately shaded or wash drawings.

The primary purpose in drawings of insects or insect structures should be accuracy. A gifted artist can make a freehand drawing that is fairly accurate, but most people need some sort of mechanical aid to obtain the needed precision. Several devices and techniques can help you turn out an accurately proportioned drawing with a minimum of effort. These include a drawing tube, a projection apparatus, cross-hatching, and careful measurements of the specimen. A drawing tube is a device that fits into the light path between the eyepiece and objective lens of a microscope. It contains a system of prisms and mirrors so arranged that, by looking through it, you see both the object under the microscope and the paper on which the drawing is to be made, and can trace exactly what you see through the microscope. It takes a little practice to learn how to use a drawing tube, but a person who has gotten the knack of it can turn out accurate drawings quite rapidly. A drawing tube is a rather expensive piece of equipment and is likely to be available only in well-equipped university research laboratories.

Any insect or insect structure that is fairly flat and translucent can be drawn by projection. The object to be drawn is projected by means of a photographic enlarger, slide projector, or other apparatus onto a sheet of paper, and the drawing is traced over the projected image. This is the ideal method of making drawings of insect wings, which can be mounted between two glass slides. Elaborate projectors can be obtained that will give magnifications of from 4× to 5× up to several hundred, but they are rather expensive. If you do not want too much magnification, you can use photographic enlargers, slide projectors, or microprojectors.

The cross-hatching principle can be used for making drawings at a different scale. The object to be drawn is observed through a grid of crossed lines and then drawn on coordinate paper, the detail of the object being put in one square at a time. For drawing a macroscopic object, a grid made of crossed threads can be set up in front of the object. For microscopic objects, a transparent disk on which fine cross-lines are etched is put into the eyepiece of the microscope. For copying a drawing at a different scale, a grid of one scale is put over the drawing to be copied, and the details of the drawing are copied one square at a time on coordinate paper that has a different scale. With a good photocopier, reductions or enlargements can also be easily made.

A wall chart or any greatly enlarged drawing can be made from a text figure either by projection or by the cross-hatching method. Text drawings can be projected by an opaque projector and traced, or they can be enlarged on a chart by using the grid principle described in the preceding paragraph.

If you do not have any of these mechanical aids, a considerable degree of accuracy can still be achieved by carefully measuring the specimen to be drawn and then making the drawing agree with these measurements. Measure small objects with dividers.

The simplest way to obtain a symmetrical drawing, when drawing an animal (or part of an animal) that is bilaterally symmetrical, is to draw only the right or left half of the specimen and then trace the other half from the first side.

Whether or not a drawing should contain some sort of shading depends on what you wish to show. Many drawings of insect structures (for example, most of the drawings in this book showing anatomical characters) show what they are intended to show without any shading, or perhaps with a few well-placed lines. If you wish to show contour or surface texture, as would be shown in a photograph, more elaborate shading is necessary. This shading may be done by stippling (a series of dots, as in Figure 5–28), parallel or crossed lines (for example, the eyes in Figure 11–11), a series of dots and lines (for example, Figure 22–46), or the use of a special type of drawing paper containing tiny raised areas (stipple board, coquille board, Ross board, and so on, which were used in preparing such drawings as those in Figures 26–53 and 26–65). Press-on sheets of various types of shading, stippling, lines, cross-hatching, and other patterns provide a quick yet satisfactory method of providing shading and texture.

Drawings prepared for publication are ordinarily made about twice the size at which they will be reproduced, sometimes larger. The subsequent reduction tends to eliminate minor irregularities in the original drawing. If the reduction is very great, however, the fine lines disappear, or lines close together on the original drawing appear run together in the printed drawing.

To learn how to prepare good drawings, study good drawings in textbooks and research papers. By studying carefully the details of such drawings, you will learn some of the tricks of giving an effect of contour with minimal shading, and you will learn the shading methods that best produce the desired effects. You will also learn something of the preferred style of arranging and labeling drawings.

Sources of Information

Information on insects is available in the form of literature published by federal and state organizations, from private organizations such as supply houses, museums, and societies, and from a great mass of books and periodicals. Much of this literature is available in a good library, and a good bit can be obtained at little or no cost to the student or teacher. Information is also available from contacts with other people who are interested in insects—amateurs and workers in universities, museums, and experiment stations. Materials such as slides, movies, and exhibits are available from supply houses, museums, and often various state or private agencies.

Electronic Resources

The World Wide Web probably provides the most accessible and most up-to-date information. The ease with which web pages can be written and their capacity for incorporating images have resulted in an explosion of the number of resources available. A quick search of Google finds 1.9 million hits for the word "insect" and 585,000 for the esoteric term "entomology." Many of these pages are of dubious quality, and the onus is on the user to determine their value. This is, however, also the situation in the traditionally published literature, even in journals carrying peer-reviewed science. The difference is only a matter of scale, in our opinion, and the real-time accessibility clearly makes the Internet, overall, a tremendous asset.

Web pages are notoriously unstable, rapidly going out of date or, worse, out of existence. For this reason, we have hesitated to recommend specific sites in this book. Most professional societies, entomology departments, extension services, and natural history museums maintain high-quality web sites containing a wide range of valuable information. As web-indexing services continue to improve, they supply the best means for rapidly locating quality material on the Internet.

Government Publications

Many government publications are available to the public free of charge. Publications are available for sale at a nominal cost. A wealth of literature on insects is available from the government.

Information on the publications of various governmental agencies can be obtained from the Division of Public Documents, Government Printing Office, Washington, DC 20402 (www.access.gpo.gov). This office publishes a number of lists of publications (one is on insects), which are available without cost. Most government publications on insects are published by the U.S. Department of Agriculture (USDA), and information on the publications of this department can be obtained from the following sources: (1) List 11, *List of the Available Publications of the U.S. Department of Agriculture* (revised every year or so), available from the U.S. Department of Agriculture, Washington, DC 20250; (2) indexes published by the USDA; and (3) indexing journals, such as the *Bibliography of Agriculture*.

State Publications

Many publications of state agencies are available free to residents of that state. In some states there are several agencies whose publications would be of interest to the student or teacher of entomology, particularly the agricultural experiment station, the extension service, the departments of education and conservation, the biological or natural history survey, and the state museum. Information on the publications available from these agencies can usually be obtained by writing directly to the agencies.

Many agricultural experiment stations are closely associated with the agricultural college and are located in the same town. The extension service is nearly always a part of the agricultural college. State departments of education or conservation are usually located in the capital. State museums are usually located in the capital or in the same town as the state university. Many state universities have museums that contain insect collections and that often publish papers on insects. State biological surveys are usually associated with the state university or agricultural college.

Miscellaneous Agencies

Biological supply houses are useful sources of equipment, material, and often publications of interest to an entomologist. All supply houses publish catalogs, which are sent free or at a nominal cost to teachers and schools. These catalogs are of value in indicating what can be obtained from the supply houses, and many of their illustrations suggest things that ingenious students or teachers can prepare themselves.

Many societies, museums, and research institutions publish material that is useful to entomologists. Entomological societies (see the following section), state biological survey organizations, and organizations such as the National Audubon Society (950 Third Ave., New York, NY 10022) will send lists of their publications on request.

Directories of Entomologists

Anyone interested in insects will find it profitable to become acquainted with others who have similar interests. A person who is located near a university, museum, or experiment station should become acquainted with the workers there who are interested in insects. People throughout the country who are interested in various phases of entomology can often be located on the Internet or by consulting the membership lists of the various entomological societies, which are usually published at intervals in the societies' journals or various directories.

Entomological Societies

There are a great many entomological societies in the United States, membership in which is generally open to anyone interested in entomology. The dues vary but are generally \$10 or more per year. Members usually receive the publications of the society, notices of meetings, and newsletters. The societies of national scope usually have meetings only once a year. Smaller local societies may have meetings at more frequent intervals.

Some of the better-known entomological societies in the United States and Canada, with their principal publications, are as follows:

American Entomological Society: *Transactions of the American Entomological Society*, *Entomological News*.
Cambridge Entomological Club: *Psyche*.
Entomological Society of America: *Annals of the Entomological Society of America, Environmental Entomology, Journal of Economic Entomology, American Entomologist*.
Entomological Society of Canada: *Canadian Entomologist, Memoirs of the Entomological Society of Canada*.
Entomological Society of Washington: *Proceedings of the Entomological Society of Washington*.
Florida Entomological Society: *The Florida Entomologist*.
Kansas (Central States) Entomological Society: *Journal of the Kansas Entomological Society*.
Michigan Entomological Society: *Great Lakes Entomologist*.
New York Entomological Society: *Journal of the New York Entomological Society*.
Pacific Coast Entomological Society, *The Pan-Pacific Entomologist*.

References

Blum, M. S., and J. P. Woodring. 1963. Preservation of insect larvae by vacuum dehydration. J. Kan. Entomol. Soc. 36:96–101.

DeLong, D. M., and R. H. Davidson. 1936. Methods of Collecting and Preserving Insects. Columbus: Ohio State University Press, 20 pp.

Gordh, G., and J. C. Hall. 1979. A critical point drier used as a method of mounting insects from alcohol. Entomol. News 90:57–59.

Hodges, E. R. S. (Ed.). 1989. The Guild Handbook of Scientific Illustration. New York: Van Nostrand Reinhold, 575 pp.

Knudson, J. W. 1972. Collecting and Preserving Plants and Animals. New York: Harper & Row, 320 pp.

Martin, J. E. H. 1977. Collecting, preparing, and preserving insects, mites, and spiders. The Insects and Arachnids of Canada, Part 1. Ottawa: Agriculture Canada, 182 pp.

Masner, L., and H. Goulet. 1981. A new model of flight-interception trap for some hymenopterous insects. Entomol. News 92:199–202.

Peck, S. B., and A. E. Davies. 1980. Collecting small beetles with large-area "window" traps. Coleop. Bull. 34:237–239.

Roe, R. M., and C. W. Clifford. 1976. Freeze-drying of spiders and immature insects using commercial equipment. Ann. Entomol. Soc. Amer. 69:497–499.

Schauff, M. E. (Ed.). 2001. Collecting and preserving insects and mites: Techniques and tools. Available on-line at www.sel.barc.usda.gov/selhome/collpres/collpress.htm. Accessed February 11, 2004.

Southwood, T. R. E. 1966. Ecological Methods, with Particular Reference to the Study of Insect Populations. London: Methuen, 391 pp.

Townes, H. 1972. A light-weight Malaise trap. Entomol. News 83: 239–247.

Woodring, J. P., and M. Blum. 1963. Freeze-drying of spiders and immature insects. Ann. Entomol. Soc. Amer. 56:138-141.

Zweifel, F. W. 1961. A Handbook of Biological Illustration. Chicago: University of Chicago Press, 131 pp.

Glossary

The definitions given here apply primarily to the use of these terms in this book; elsewhere some terms may have additional or different meanings. Some terms not listed here may be found in the Index.

abdomen The posterior of the three body divisions (Figure 2–1, ab).

accessory cell A closed cell in the front wing of Lepidoptera formed by the fusion of two branches of the radius, usually the R_2 cell (Figure 30–17, acc).

accessory gland A secretory organ associated with the reproductive system.

accessory pulsatile organ Contractile organs that function to move hemolymph into and out of appendages.

accessory vein An extra branch of a longitudinal vein (indicated by a subscript *a;* for example, an accessory of M_1 is designated M_{1a}).

acrosternite The part of a sternum anterior to the antecostal suture.

acrostichal bristles One or more longitudinal rows of small bristles along the center of the mesonotum (Diptera; Figure 34–6, acr).

acrotergite The part of a tergum anterior to the antecostal suture.

aculea (pl., *aculeae*) Minute spines on the wing membrane (Lepidoptera).

aculeate With aculeae (Lepidoptera); with a sting (Hymenoptera).

acuminate Tapering to a long point.

acute Pointed; forming an angle of less than 90 degrees.

adecticous A type of pupa in which the mandibles are immovable and nonfunctional.

adfrontal areas A pair of narrow, oblique sclerites on the head of a lepidopterous larva (Figure 30–3, adf).

adventitious vein A secondary vein, neither accessory nor intercalary, usually the result of crossveins lined up to form a continuous vein.

aedeagus The male intromittent organ; the distal part of the phallus; penis plus parameres.

aestivation Dormancy during a warm or dry season.

agamic Reproducing parthenogenetically, that is, without mating.

alinotum The notal plate of the mesothorax or metathorax of a pterygote insect (Figure 2–6, AN).

alula (pl., *alulae*) A lobe at the base of the wing (Diptera; Figure 34–4, alu); see **calypter.**

ametabolous Without metamorphosis.

anal Pertaining to the last abdominal segment (which bears the anus); the posterior basal part (for example, of the wing).

anal area of the wing The posterior portion of the wing, usually including the anal veins.

anal cell A cell in the anal area of the wing; cell 1A (Diptera; Figure 34–4B, A).

anal crossing Where A branches posteriorly from Cu+A (Odonata; Figure 10–5, Ac).

anal lobe A lobe in the posterior basal part of the wing.

anal loop A group of cells in the hind wing of dragonflies, between Cu_2, 1A, and 2A, which may be rounded (Figure 10–7B), elongate (Figure 10–7C), or foot-shaped (Figure 10–5, alp).

anapleurite The upper and outer of the two incomplete subcoxal rings that form the thoracic pleurites.

anepimeron The part of the anapleurite posterior to the pleural suture.

anepisternum The part of the anapleurite anterior to the pleural suture.

annulated With ringlike segments or divisions.

annulated antenna An antenna composed of three segments, the scape, pedicel, and flagellum; the apical flagellum is often subdivided (annulated); characteristic of true insects.

anteapical Just proximad of the apex.

anteapical cell A cell in the distal part of the wing (leafhoppers; Figure 22–11, table).

anteclypeus An anterior division of the clypeus (Figure 10–8, aclp).

antecosta (pl., *antecostae*) An internal ridge on the anterior portion of a tergum or sternum that serves as the site of attachment for the longitudinal muscles.

antecostal suture An external groove that marks the position of the internal antecosta.

antecoxal sclerite A sclerite of the metasternum, just anterior to the hind coxae.

antenna (pl., *antennae*) A pair of segmented appendages located on the head above the mouthparts and usually sensory in function (Figure 2–15).

antennal club The enlarged distal segments of a clubbed antenna (Figure 26–3B, acl).

antennal fossa A cavity or depression in which the antennae are located (Figure 34–5, af).

antennal groove A groove in the head capsule into which the basal segment of the antenna fits (Figure 26–3, agr).

antennifer A small process on the head with which the antenna articulates.

antennule The first antennae of Crustacea (Figure 5–24, antl).

antenodal crossveins Crossveins along the costal border of the wing, between the base of the wing and the nodus, extending from the costa to the radius (Odonata; Figure 10–5, an).

antepenultimate The third from the last.

antepygidial bristle One or more large bristles on the apical margin of the seventh (next to the last) tergum (Siphonaptera).

anterior Front; in front of.

anterior crossvein The r-m crossvein (Diptera; Figure 34–4B, acv).

anterodorsal In the front and at the top or upper side.

anteromesal In the front and along the midline of the body.

anteroventral In the front and underneath or on the lower side.

anus The posterior opening of the alimentary tract (Figure 2–22, ans).

aorta The anterior nonpulsatile portion of the dorsal blood vessel.

apical At the end, tip, or outermost part.

apical cell A cell near the wing tip (Figure 22–50; Figure 34–4B, SM; Figure 28–3, AP).

apical crossvein A crossvein near the apex of the wing (Plecoptera, Figure 16–7D, apc; Hemiptera, Figure 22–11, table).

apodeme An invagination of the body wall forming a rigid process that serves for muscle attachment and for the strengthening of the body wall.

apolysis The separation of the epidermis from the cuticle (part of the process of molting).

apomorphy A derived character, that is, one that is changed from the ancestral condition.

apophysis (pl., *apophyses*) A tubercular or elongate process of the body wall, either external or internal (Figure 2–4, apo).

appendix A supplementary or additional piece or part (of the hemipteran wing, see Figure 22–11, ap).

appressed setae Setae that lie parallel to or in contact with the body surface.

apterous Wingless.

apterygote A primitively wingless hexapod.

aquatic Living in water.

arcuate Bent like a bow, or arched.

arculus A basal crossvein between the radius and the cubitus (Odonata; Figures 10–5 through 10–7, arc).

areole An accessory cell (see also basal areole).

areolet A small cell in the wing; in the Ichneumonidae, the small, submarginal cell opposite the second m-cu crossvein (Figure 28–31, are).

arista A large bristle, usually dorsally located, on the apical antennal segment (Diptera; Figure 34–5, ar).

aristate Bristlelike; with an arista; aristate antenna (Figures 2–15J, 34–19A,B).

arolium (pl., *arolia*) A padlike structure at the apex of the last tarsal segment, between the claws (Orthoptera; Figure 11–4C, aro); a padlike structure at the base of each tarsal claw (Hemiptera; Figures 22–1, 22–3A, aro).

arrhenotoky A form of parthenogenesis in which females are produced from fertilized eggs, males from unfertilized eggs.

articulation A joint as between two segments or structures.

aspirator A device with which insects may be picked up by suction (Figure 35–3).

asymmetrical Not alike on the two sides.

asynchronous muscle A rapidly contracting muscle in which the individual contractions are not initiated by a neuronal impulse (compare with synchronous or neurogenic muscle).

atrium (pl., *atria*) A chamber; a chamber just inside a body opening.

atrophied Reduced in size, rudimentary.

attenuated Very slender and gradually tapering distally.

auricle A small lobe or earlike structure (Hymenoptera; Figure 28–66, au).

auxiliary vein The subcosta (Diptera; Figure 34–4, av).

axilla (pl., *axillae*) A triangular or rounded sclerite laterad of the scutellum and usually just caudad of the base of the front wing (Hymenoptera; Figure 28–4, ax).

axillary cell A cell in the anal area of the wing (Diptera, Figure 34–4, axc; Hymenoptera, Figure 28–3, AX).

axillary sclerites The small sclerites at the base of the wing that translate deformations of the thorax into wing movements (Figure 2–11, axs).

band A transverse marking broader than a line.

basad Toward the base.

basal anal cell An anal cell near the wing base; a cell at the base of the wing between 1A and 2A (Plecoptera; Figure 16–1, BA).

basal areole A small cell at the base of the wing; the cell at the base of the wing between Sc and R (Lepidoptera; Figures 30–26 through 30–28, BA).

basal cell A cell near the base of the wing, bordered at least in part by the unbranched portions of the longitudinal veins; in the Diptera, one of the two cells proximad of the anterior crossvein and the discal cell (Diptera, Figure 34–4B, B; Hymenoptera, see Figure 28–8, B).

basal vein A vein in about the middle of the front wing, extending from the median vein to the subcostal or cubital vein; the first free segment of M (Hymenoptera; Figure 28–3, 3, bv).

basalare (or *basalar sclerite*) An epipleurite located anterior to the pleural wing process.

basement membrane A noncellular membrane underlying the epidermal cells of the body wall (Figures 2–2, 2–4, bm).

basisternum The part of a thoracic sternum anterior to the sternacostal suture.

beak The protruding mouthpart structures of a sucking insect; proboscis (Figures 2–17 through 2–20, bk).

bifid Forked, or divided into two parts.

bilateral symmetry See **symmetry**.

bilobed Divided into two lobes.

bipectinate Having branches on two sides like teeth of a comb.

biramous With two branches; consisting of an endopodite and an exopodite (Crustacea).

bisexual With males and females.

bituberculate With two tubercles or swellings.

bivalved With two valves or parts, clamlike.

blastoderm The peripheral cell layer in the insect egg following cleavage (Figure 2–37C, bl).

book gills The leaflike gills of a horseshoe crab (Figure 5–2, bg).

book lung A respiratory cavity containing a series of leaflike folds (spiders).

borrow pit A pit formed by an excavation, where earth has been "borrowed" for use elsewhere.

boss A smooth, lateral prominence at the base of a chelicera (spiders).

brace vein A slanting crossvein; in Odonata, a slanting crossvein just behind the proximal end of the stigma (Figure 10–7E, bvn).

brachypterous With short wings that do not cover the abdomen.

brain The anterior ganglion of the nervous system, located above the esophagus; in insects, consisting of the protocerebrum, deutocerebrum, and tritocerebrum.

brain hormone A chemical messenger produced by neurosecretory cells in the brain that activates the prothoracic glands to produce ecdysone (also known as *PTTH* or *prothoracicotropic hormone*).

bridge crossvein A crossvein anterior to the bridge vein (Odonata; Figure 10–5, bcv).

bridge vein The vein that appears as the basal part of the radial sector, between M_{1+2} and the oblique vein (Odonata; Figure 10–5, brv).

brood The individuals that hatch from the eggs laid by one mother; individuals that hatch at about the same time and normally mature at about the same time.

bucca (pl., *buccae*) A sclerite on the head below the compound eye and just above the mouth opening (Diptera; Figure 34–5, buc).

buccula (pl., *bucculae*) One of two ridges on the underside of the head, on each side of the beak (Hemiptera; Figures 2–17, 22–1, buc).

bursa copulatrix A pouch of the female reproductive system that receives the male genitalia during copulation.

bursicon A hormone involved in the process of sclerotization.

caecum (pl., *caeca*) A saclike or tubelike structure, open at only one end.

calamistrum One or two rows of curved spines on the metatarsus of the hind legs (spiders; Figure 5–7, CA).

calcaria Movable spurs at the apex of the tibia (Figure 11–4F, G, clc).

callus (pl., *calli*) A rounded swelling.

calypter (pl., *calypteres*) One or two small lobes at the base of the wing, located just above the haltere (Diptera; Figure 34–4, cal) (see also **squama**).

camera lucida A device enabling one to make accurate drawings of objects seen through a microscope; when it is attached to the eyepiece of a microscope the observer can see both the object under the microscope and the drawing paper at the same time.

campaniform sensillum A sense organ consisting of a dome-shaped cuticular area into which the sensory cell process is inserted like the clapper of a bell (Figure 2–27B).

campodeiform larva A larva shaped like the dipluran Campodea (Figure 7–4A), that is, elongate and flattened, with well-developed legs and antennae, and usually active.

canthus A cuticular process that subdivides the eye (Coleoptera).

capitate With a knoblike apical enlargement; capitate antenna (Figure 2–15F).

carapace A hard dorsal covering consisting of fused dorsal sclerites (Crustacea; Figure 5–22, crp).

cardo (pl., *cardines*) The basal segment or division of a maxilla (Figure 2–16A, cd); one of two small laterobasal sclerites in the millipede gnathochilarium (Figure 5–30B, cd).

carina (pl., *carinae*) A ridge or keel.

carinate Ridged or keeled.

carnivorous Feeding on the flesh of other animals.

caste A form or type of adult in a social insect (termites, see Figure 19–2; ants, see Figure 28–83).

catapimeron The portion of the catapleurite posterior to the pleural suture.

catapleurite The lower and inner of the two incomplete subcoxal rings that form the thoracic pleurites (also called the *catepleurite, katepleurite,* and *coxopleurite*).

catepisternum The portion of the catapleurite anterior to the pleural sulcus.

caterpillar An eruciform larva; the larva of a butterfly (Figure 30–3), moth, sawfly, or scorpionfly.

caudad Toward the tail, or toward the posterior end of the body.

caudal Pertaining to the tail or posterior end of the body.

caudal filament A threadlike process at the posterior end of the abdomen.

cell A space in the wing membrane partly (an open cell) or completely (a closed cell) surrounded by veins.

cenchrus (pl., *cenchri*) Roughened pad on the metanotum of sawflies (Symphyta) serving to hold the wings in place when folded over the dorsum.

cephalad Toward the head or anterior end.

cephalic On or attached to the head; anterior.

cephalothorax A body region consisting of head and thoracic segments (Crustacea and Arachnida; Figure 5–6).

cercus (pl., *cerci*) One of a pair of appendages at the posterior end of the abdomen (Figure 2–1, cr).

cervical Pertaining to the neck or cervix.

cervical sclerite A sclerite located in the lateral part of the cervix, between the head and the prothorax (Figure 2–6, cvs).

cervix The neck, a membranous region between the head and prothorax (Figure 2–6, cvx).

chaetotaxy The arrangement and nomenclature of the bristles on the exoskeleton (Diptera; Figures 34–5, 34–6).

cheek The lateral part of the head between the compound eye and the mouth (see **gena**).

chelate Pincerlike, having two opposable claws.

chelicera (pl., chelicerae) One of the anterior pair of appendages in arachnids (Figure 5–6).

cheliped A leg terminating in an enlarged pincerlike structure (Crustacea; Figure 5–22).

chemoreceptor A sensillum capable of detecting chemicals (by olfaction and/or gustation).

chitin A nitrogenous polysaccharide formed primarily of units of N-acetyl glucosamine, occurring in the cuticle of arthropods.

chordotonal organ A sense organ, the cellular elements of which form an elongate structure attached at both ends to the body wall.

chorion The outer shell of an arthropod egg.

chrysalis (pl., *chrysalids* or *chrysalides*) The pupa of a butterfly (Figure 30–4, A,B).

cibarium A preoral cavity enclosed by the labrum anteriorly, the hypopharynx or labium posteriorly, and the mandibles and maxillae laterally.

circumesophageal connective A nerve connecting the tritocerebral lobes of the brain with the subesophageal ganglion (Figure 2–22, cec).

cladistics School of systematics that seeks to recognize monophyletic groups on the basis of shared derived characters.

cladogram A branching diagram that represents the distribution of derived character states (apomorphies, homologies) among taxa; by extension, the cladogram then represents the relationships among those taxa and their evolutionary history.

class A subdivision of a phylum or subphylum, containing a group of related orders.

claval suture The suture of the front wing separating the clavus from the corium (Hemiptera; Figure 22–1, cls).

claval vein A vein in the clavus (Hemiptera; Figure 22–10, clv).

clavate Clublike, or enlarged at the tip; clavate antennae (Figure 2–15D,E).

clavus The oblong or triangular anal portion of the front wing (Hemiptera; Figures 22–1, 22–4 cl).

claw tuft A dense tuft of hairs below the claws (spiders; Figure 5–7E, CT).

cleft Split or forked.

closed cell A wing cell bounded on all sides by veins.

closed coxal cavity One bounded posteriorly by a sclerite of the same thoracic segment (front coxal cavities, Coleoptera; Figure 26–7B), or one completely surrounded by sternal sclerites and not touched by any pleural sclerites (middle coxal cavities, Coleoptera; Figure 26–7D).

clubbed With the distal part (or segments) enlarged; clubbed antennae (Figure 2–15D-F,L,M).

clypeus A sclerite on the lower part of the face, between the frons and the labium (Figure 2–13, clp).

coarctate larva A larva somewhat similar to a dipterous puparium, in which the skin of the preceding instar is not completely shed but remains attached to the caudal end of the body; the sixth instar of a blister beetle, see also **pseudopupa** (Figure 26–68H).

coarctate pupa A pupa enclosed in a hardened shell formed by the next-to-last larval skin (Diptera; Figure 2–44F).

cocoon A silken case inside which the pupa is formed.

collophore A tubelike structure on the ventral side of the first abdominal segment of most Collembola.

collum The tergite of the first segment (Diplopoda; Figure 5–30A, colm).

colon The large intestine; that part of the hindgut between the ileum and the rectum (Figure 2–22, cn).

colulus A slender, pointed structure lying just anterior to the spinnerets (spiders).

commensalism A living together of two or more species, none of which is injured thereby, and at least one of which is benefited.

commissure A structure (trachea or nerve) that connects the left and right sides of a segment.

common oviduct The median tube of the female internal genitalia leading from the lateral oviducts to the gonopore.

compound eye An eye composed of many individual elements or ommatidia, each represented externally by a facet; the external surface of such an eye consists of circular facets that are very close together or of facets that are in contact and more or less hexagonal in shape (Figure 2–1, e, Figure 2–29C,D).

compressed Flattened from side to side.

concave vein A vein protruding from the lower surface of the wing.

condyle A knoblike process forming an articulation.

connate Fused together or immovably united.

connective A structure (such as a trachea or nerve) that runs from one segment to another.

constricted Narrowed.

contiguous Touching each other.

convergent Becoming closer distally.

convex vein A vein protruding from the upper surface of the wing.

corbicula (pl., *corbiculae*) A smooth area on the outer surface of the hind tibia, bordered on each side by a fringe of long, curved hairs, which serves as a pollen basket (bees).

corium The elongate, usually thickened, basal portion of the front wing (Hemiptera; Figure 22–4, cor).

cornea The cuticular part of an eye (Figure 2–29, cna).

cornicle One of a pair of dorsal tubular structures on the posterior part of the abdomen (aphids; Figure 22–14C, crn).

corniculi (sing., *corniculus*) See **urogomphi**.

coronal suture A longitudinal suture along the midline of the vertex, between the compound eyes (Figure 2–13, cs).

corpus allatum (pl., *corpora allata*) One of a pair of small structures immediately behind the brain, involved in secretion of juvenile hormone (Figure 2–26, ca).

costa (pl., *costae*) A longitudinal wing vein usually forming the anterior margin of the wing (Figure 2–10, C); a sclerotized ridge in the cuticle.

costal area The portion of the wing immediately behind the anterior margin.

costal break A point on the costa where the sclerotization is weak or lacking or the vein appears to be broken (Diptera; Figures 34–22A,B, 34–24C–E, cbr).

costal cell The wing space between the costa and the subcosta.

coxa (pl., *coxae*) The basal segment of the leg (Figure 2–8, cx).

coxopleurite See **catapleurite**.

coxopodite The basal segment of an arthropod appendage.

coxosternum A sclerite representing the fusion of the sternum and the coxopodites of a segment.

crawler The active first instar of a scale insect (Figure 22–63B).

cremaster A spinelike or hooked process at the posterior end of the pupa, often used for attachment (Lepidoptera; Figure 30–4, cre).

crenulate Wavy, or with small scallops.

cribellum A sievelike structure lying just anterior to the spinnerets (spiders; Figure 5–8A, CR).

crochets (pronounced croshays) Hooked spines at the tip of the prolegs of lepidopterous larvae (Figure 30–3, cro).

crop The dilated posterior portion of the foregut, just behind the esophagus (Figure 2–22, cp).

crossvein A vein connecting adjacent longitudinal veins.

cruciate Crossing; shaped like a cross.

cryptonephridia Malpighian tubules that are closely associated with the hind gut and surrounded by a membrane, thus separating this complex from the rest of the hemocoel.

ctenidium (pl., *ctenidia*) A row of stout bristles like the teeth of a comb.

cubito-anal crossvein A crossvein between the cubitus and an anal vein (Figure 2–10, cu-a).

cubitus The longitudinal vein immediately posterior to the media (Figure 2–10, Cu).

cuneus A more or less triangular apical piece of the corium, set off from the rest of the corium by a suture (Hemiptera; Figure 22–4, cun).

cursorial Fitted for running; running in habit.

cuticle (or *cuticula*) The noncellular outer layer of the body wall of an arthropod (Figures 2–2, 2–4, cut).

cymbium The tarsus of the pedipalp of a male spider.

cyst A sac, vesicle, or bladderlike structure.

deciduous Having a part or parts that may fall off or be shed.

decticous A type of pupa with movable, functional mandibles.

decumbent Bent downward.

deflexed Bent downward.

dens (pl., *dentes*) The central segment of the furcula of Collembola, attached to the manubrium basally and with the mucro attached apically.

dentate Toothed, or with toothlike projections.

denticulate With minute, toothlike projections.

depress To lower an appendage (e.g., leg or wing).

depressed Flattened dorsoventrally.

desmosome One form of subcellular attachment between the plasma membranes of two adjacent cells.

deutocerebrum The middle pair of lobes of the brain, innervating the antennae.

deutonymph The third instar of a mite (Figure 5–17D).

diapause A period of arrested development and reduced metabolic rate, during which growth, differentiation, and metamorphosis cease; a period of dormancy not immediately referable to adverse environmental conditions.

dichoptic The eyes separated above (Diptera).

dicondylic A joint with two points of articulation.

diecious Having the male and female organs in different individuals, any one individual being either male or female.

dilated Expanded or widened.

direct flight mechanism Generation of wing movements by means of muscles pulling on the base of the wings.

disc The central dorsal portion of the pronotum (Hemiptera).

discal cell A more or less enlarged cell in the basal or central part of the wing (Hemiptera, the R cell, Figure 22–11; Lepidoptera, Figure 30–6, D; Diptera, Figure 34–4B, D).

discal crossvein A crossvein behind the discal cell (Diptera; Figure 34–4B, dcv).

distad Away from the body, toward the end farthest from the body.

distal Near or toward the free end of an appendage; that part of a segment or appendage farthest from the body.

diurnal Active during the daytime.

divaricate Extending outward and then curving inward toward each other distally (divaricate tarsal claws; Figure 26–10A).

divergent Becoming more separated distally.

dormancy A state of quiescence or inactivity.

dorsad Toward the back or top.

dorsal Top or uppermost; pertaining to the back or upper side.

dorsal blood vessel Median upper tube that forms the primary portion of the circulatory system of arthropods.

dorsal diaphragm An incomplete wall of muscle separating the area around the dorsal blood vessel (the pericardial sinus) from the rest of the hemocoel.

dorsal longitudinal muscles One of the primary sets of segmental muscles inserted on the antecostae of successive segments (phragmata in the thorax) dorsally and the sternum ventrally, in pterothoracic segments contraction results in arching of the notum and contributes significantly to depression of the wings.

dorsocentral bristles A longitudinal row of bristles on the mesonotum, just laterad of the acrostichal bristles (Diptera; Figure 34–6, dc).

dorsolateral At the top and to the side.

dorsomesal At the top and along the midline.

dorsoscutellar bristles A pair of bristles on the dorsal portion of the scutellum, one on each side of the midline (Diptera).

dorsoventral From top to bottom, or from the upper to the lower side.

dorsum The back or top (dorsal) side.

Dyar's rule The increase in width of the larval head capsule by a factor of 1.2 to 1.4 from one molt to the next.

ecdysis (pl., *ecdyses*) Molting; the process of shedding the exoskeleton.

ecdysone (or ecdysteroid) Hormone produced by the prothoracic glands that initiates apolysis.

eclosion Hatching from the egg.

ectoparasite A parasite that lives on the outside of its host.

ejaculatory duct The terminal portion of the male sperm duct (Figure 2–31B, ejd).

elateriform larva A larva resembling a wireworm, that is, slender, heavily sclerotized, with short thoracic legs, and with few body hairs (Figure 26–45B).

elbowed antenna An antenna with the first segment elongated and the remaining segments coming off the first segment at an angle (Figure 2–15N).

elevate To raise an appendage (e.g., leg or wing).

elytron (pl., *elytra*) A thickened, leathery, or horny front wing (Coleoptera, Dermaptera, some Hemiptera; Coleoptera, Figure 26–1, el).

emarginate Notched or indented.

embolium A narrow piece of the corium, along the costal margin, separated from the rest of the corium by a suture (Hemiptera; Figure 22–4C, emb).

embolus Structure of the pedipalp of a male spider bearing the apex of the sperm duct.

emergence The act of the adult insect leaving the pupal case or the last nymphal skin.

empodium (pl., *empodia*) A padlike or bristlelike structure at the apex of the last tarsal segment, between the claws (Diptera; Figure 34–2, emp).

endite The basal segment of the spider pedipalp, which is enlarged and functions as a crushing jaw (Figure 5–6B, C).

endocuticle (or *endocuticula*) The innermost and unsclerotized layer of the cuticle (Figure 2–2, end).

endoparasite A parasite that lives inside its host (for example, Figure 34–72B).

endophallus The inner eversible lining of the male aedeagus.

endopodite The mesal branch of a biramous appendage (Figure 5–1, enp).

endopterygote Having the wings developing internally; with complete metamorphosis.

endoskeleton A skeleton or supporting structure on the inside of the body.

entire Without teeth or notches, with a smooth outline.

entomophagous Feeding on insects.

epicranium The upper part of the head, from the face to the neck (Lepidoptera; Figure 30–3, epcr).

epicuticle (or epicuticula) The very thin, nonchitinous, external layer of the cuticle (Figure 2–2, epi).

epidermis The cellular layer of the body wall, which secretes the cuticle (Figure 2–2, 2–4, ep).

epigastric furrow A transverse ventral suture near the anterior end of the abdomen, along which lie the openings of the book lungs and the reproductive organs (spiders; Figure 5–6B, C).

epigynum The external female genitalia of spiders (Figure 5–6B).

epimeron (pl., *epimera*) The area of a thoracic pleuron posterior to the pleural suture (Figure 2–6, epm).

epipharynx A mouthpart structure on the inner surface of the labrum or clypeus; in chewing insects, a median lobe on the posterior (ventral) surface of the labrum.

epiphysis (pl., *epiphyses*) A movable pad or lobelike process on the inner surface of the front tibia (Lepidoptera).

epiphyte An air plant, one growing nonparasitically on another plant or on a nonliving object.

epipleura (pl., *epipleurae*) The bent-down lateral edge of an elytron (Coleoptera).

epipleurite A small sclerite in the membranous area between the thoracic pleura and the wing bases (Figure 2–6, epp).

epiproct A process or appendage situated above the anus and appearing to arise from the tenth abdominal segment; actually, the dorsal part of the eleventh abdominal segment (Figure 2–1, ept).

episternum (pl., *episterna*) The area of a thoracic pleuron anterior to the pleural suture (Figure 2–6, eps).

epistomal suture (or *epistomal sulcus*) The sulcus between the frons and the clypeus (Figure 2–13, es), connecting the anterior tentorial pits.

epistome The part of the face just above the mouth; the oral margin (Diptera).

eruciform larva A caterpillar; a larva with a more or less cylindrical body, a well-developed head, and thoracic legs and abdominal prolegs (Figure 30–3).

esophagus The narrow portion of the alimentary tract immediately posterior to the pharynx (Figure 2–22, eso).

estivation See aestivation.

eusocial A condition of group living in which there is cooperation among members in rearing young, reproductive division of labor, and overlap of generations.

eusternum The ventral plate of a thoracic segment exclusive of the spinasternum.

evagination An outpocketing, or saclike structure on the outside.

eversible Capable of being everted or turned outward.

exarate pupa A pupa in which the appendages are free and not glued to the body (Figure 2–44C–E).

excavated Hollowed out.

excretion The elimination of metabolic wastes from the body.

exocuticle (or exocuticula) The layer of sclerotized cuticle just outside the endocuticle, between the endocuticle and the epicuticle (Figure 2–2, exo).

exopodite The outer branch of a biramous appendage (Figure 5–1, exp).

exopterygote With the wings developing on the outside of the body, as in insects with simple metamorphosis.

exoskeleton A skeleton or supporting structure on the outside of the body.

exserted Protruding or projecting from the body.

external The outside, that part away from the center (midline) of the body.

exuvium (pl., *exuvia*) The cast skin of an arthropod.

eye, compound See compound eye.

eye, simple See **ocellus.**

eye cap A structure overhanging or capping the compound eye (Lepidoptera; Figure 30–29B, ec).

face The front of the head, below the frontal suture (Diptera; Figure 34–5, fa).

facet The external surface of an individual compound-eye unit or ommatidium.

falx An interantennal suture with internal sclerotized margins connecting the upper ends of the antennal fossae (Siphonaptera).

family A subdivision of an order, suborder, or superfamily, containing a group of related genera, tribes, or subfamilies. Family names of animals end in *-idae.*

fastigium The anterior dorsal surface of the vertex (grasshoppers).

fat body An amorphous organ involved in intermediate metabolism, storage, and storage excretion.

feces Excrement, the material passed from the alimentary tract through the anus.

felt line A narrow, longitudinal band of relatively dense, closely appressed hairs (Mutillidae).

femur (pl., *femora)* The third leg segment, located between the trochanter and the tibia (Figure 2–8, fm).

fibula A more or less triangular jugal lobe in the front wing that serves as a means of uniting the front and hind wings (Lepidoptera; Figure 30–34, fib).

filament A slender, threadlike structure.

file A filelike ridge on the ventral side of the tegmen, near the base; a part of the stridulating mechanism in crickets and katydids (Figure 11–2).

filiform Hairlike or threadlike, filiform antenna (Figure 2–15B).

filter chamber A modification of the alimentary canal in Homoptera in which the anterior portion of the midgut is closely associated with the hindgut (Figure 2–23).

flabellate With fanlike processes or projections; flabellate antenna (Figure 2–15L).

flabellum (pl., *flabella)* A fanlike or leaflike process (Hymenoptera; Figure 28–6, flb).

flagellomere One subsegment of the flagellum.

flagellum (pl., *flagella)* A whiplike structure; that part of the antenna beyond the second segment (Figure 2–15N, fl).

flexor muscle A muscle that decreases the angle between two segments of an appendage.

foliaceous Leaflike.

follicle A minute cavity, sac, or tube.

follicular epithelium Layer of epithelial cells surrounding the oocyte.

fontanelle A small, depressed, pale spot on the front of the head between the eyes (Isoptera; Figure 19–3, fon).

foramen magnum The opening on the posterior side of the head, through which pass the internal structures that extend from head to thorax (Figure 2–13, for); also occipital foramen.

foregut Anterior portion of the alimentary tract, from the mouth to the midgut.

fossorial Fitted for or with the habit of digging.

frass Plant fragments made by a wood-boring insect, usually mixed with excrement.

frenulum A bristle or group of bristles arising at the humeral angle of the hind wing (Lepidoptera; Figure 30–6, f).

frons The head sclerite bounded by the frontal (or frontogenal) and epistomal sulci and including the median ocellus (Figure 2–13, fr).

front That portion of the head between the antennae, eyes, and ocelli; the frons.

frontal bristles Bristles above the antennae, away from the edge of the compound eye (Diptera; Figure 34–27B, fb).

frontal lunule A small, crescent-shaped sclerite located just above the base of the antennae and below the frontal suture (Diptera; Figure 34–5, frl).

frontal suture One of two sutures arising at the anterior end of the coronal suture and extending ventrad toward the epistomal sulcus (Figure 2–13, fs); a suture shaped like an inverted U, with the base of the U crossing the face above the bases of the antennae and the arms of the U extending downward on each side of the face (Diptera, Figure 34–5, fs; actually a ptilinal suture).

frontal vitta Area on the head between the antennae and the ocelli (Diptera; Figure 34–5; fv).

frontogenal suture (or *frontogenal sulcus)* A more or less vertical suture on the front of the head, between the frons and the gena.

fronto-orbital bristles Bristles on the front next to the compound eyes (Diptera; Figure 34–5, fob).

funiculus (or funicle) The antennal segments between the scape and the club (Coleoptera), or between the pedicel and club (Hymenoptera).

furca A fork or forked structure; a forked apodeme arising from a thoracic sternum (Figure 2–7, fu).

furcula The forked springing apparatus of the Collembola.

galea The outer lobe of the maxilla, borne by the stipes (Figure 2–16A, g).

gall An abnormal growth of plant tissues, caused by the stimulus of an animal or another plant.

ganglion (pl., *ganglia)* A knotlike enlargement of a nerve, containing a coordinating mass of nerve cells (Figure 2–22, gn).

gaster The rounded part of the abdomen posterior to the nodelike segment or segments (Hymenoptera Apocrita).

gastric caecum Caecum located at the anterior portion of the midgut.

gena (pl., *genae)* The part of the head on each side below and behind the compound eyes, between the frontal and occipital sulci (Figure 2–13, ge).

genal comb A row of strong spines on the anteroventral border of the head (Siphonaptera; Figure 31–1).

generation From any given stage in the life cycle to the same stage in the offspring.

geniculate Elbowed, or abruptly bent; geniculate antenna (Figure 2–15N).

genital chamber See **bursa copulatrix.**

genitalia The sexual organs and associated structures; the external sexual organs (Figures 2–32, 2–33).

genovertical plate An area on the head above the antenna and next to the compound eye (Diptera; Figure 34–5, gvp, 34–23C, orp), also called *orbital plate*.

genus (pl., *genera*) A group of closely related species; the first name in a binomial or trinomial scientific name. Names of genera are latinized, capitalized, and when printed are italicized.

germarium Apical portion of the ovariole or sperm follicle.

gill Evagination of the body wall or hindgut, functioning in gaseous exchanges in an aquatic animal.

glabrous Smooth, without hairs.

globose, globular Spherical or nearly so.

glossa (pl., *glossae*) One of a pair of lobes at the apex of the labium between the paraglossae (Figure 2–16C, gl); in bees, see Figure 28–6.

gnathochilarium A platelike mouthpart structure in the Diplopoda, representing the fused maxillae and labium.

gonangulum A sclerite of the female external genitalia derived from the second gonocoxa, connecting the second gonocoxa, ninth tergum, and first gonapophysis.

gonapophysis (pl., *gonapophyses*) A mesal posterior process of a gonopod, in the female forming the ovipositor (see Figures 2–32, gap; 8–1); first or second valvula.

gonobase The basal portion of the male external genitalia from which the paramers and aedeagus arise; usually ring-shaped.

gonocoxa A modified coxa that forms a part of the external genitalia (= valvifer).

gonoplacs Lateral sheaths enveloping the ovipositor in pterygotes (= third valvulae).

gonopod A modified leg that forms a part of the external genitalia.

gonopore The external opening of the reproductive organs.

gonostylus Stylus of a genital segment (abdominal segment 8 or 9).

gregarious Living in groups.

grub A scarabaeiform larva; a thick-bodied larva with a well-developed head and thoracic legs, without abdominal prolegs, and usually sluggish (Figures 2–43B, 26–31).

gula A sclerite on the ventral side of the head between the labium and the foramen magnum (Figure 26–4, gu).

gular sutures Longitudinal sutures, one on each side of the gula (Figure 26–4, gs).

gustation Taste, detection of chemicals in liquid.

gynandromorph An abnormal individual containing structural characteristics of both sexes (usually male on one side and female on the other).

haltere (pl., *halteres*) A small knobbed structure on each side of the metathorax, formed from a modified hind wing (Diptera; Figure 6–4, hal).

hamuli (sing., *hamulus*) Minute hooks; a series of minute hooks on the anterior margin of the hind wing, with which the front and hind wings are attached together (Hymenoptera).

haustellate Formed for sucking, the mandibles not fitted for chewing (or absent).

haustellum A part of the beak (Diptera; Figures 2–19, 2–20, hst).

head The anterior body region, which bears the eyes, antennae, and mouthparts (Figure 2–1, hd).

heart The posterior pulsatile portion of the dorsal blood vessel.

hemelytron (pl., *hemelytra*) The front wing of Hemiptera (Heteroptera) (Figure 22–4).

hemimetabolous Having simple metamorphosis, like that in the Odonata, Ephemeroptera, and Plecoptera (with the nymphs aquatic).

hemocoel A body cavity filled with blood.

hemocyte A blood cell.

hemolymph The blood of arthropods.

herbivorous Feeding on plants.

hermaphroditic Having both male and female sex organs.

hertz Cycles per second (Hz).

heterodynamic life cycle A life cycle in which there is a period of dormancy.

heterogamy Alternation of bisexual with parthenogenetic reproduction.

heteromerous The three pairs of tarsi differing in the number of segments (Coleoptera, for example, with a tarsal formula of 5–5–4).

hibernation Dormancy during the winter.

hindgut The posterior portion of the alimentary tract, between the midgut and the anus.

holocrine secretion Release of enzymes by disruption of the entire cell.

holometabolous With complete metamorphosis.

holoptic The eyes contiguous above (Diptera).

holotype A specimen designated by the author of a new species or subspecies to which the scientific name is attached. If it is found that this specimen belongs to another species or subspecies, then the original name becomes a synonym of the second name.

homodynamic life cycle A life cycle in which there is continuous development, without a period of dormancy.

homologize To recognize that two characters are derived from the same ancestral character.

homology A character that is shared between two species because both inherited it from their common ancestor.

homonym One name for two or more different things (taxa).

honeydew Liquid discharged from the anus of certain Hemiptera.

hornworm A caterpillar (larva of Sphingidae) with a dorsal spine or horn on the last abdominal segment (Figure 30–78).

horny Thickened or hardened.

host The organism in or on which a parasite lives; the plant on which an insect feeds.

humeral Pertaining to the shoulder; located in the anterior basal portion of the wing.

humeral angle The basal anterior angle or portion of the wing.

humeral bristles The bristles on the humeral callus (Diptera; Figure 34–6, hb).

humeral callus One of the anterior lateral angles of the thoracic notum, usually more or less rounded (Diptera; Figure 34–6, hc).

humeral crossvein A crossvein in the humeral portion of the wing, between the costa and subcosta (Figure 2–10, h).

humeral suture The mesopleural suture (Odonata; Figure 10–4, pls_2).

humeral vein A branch of the subcosta that serves to strengthen the humeral angle of the wing (Neuroptera, Figure 27–2C, hv; Lepidoptera, Figure 30–23B, hv).

humerus (pl., *humeri*) The shoulder; the posterolateral angles of the pronotum (Hemiptera).

hyalline Like glass, transparent, colorless.

hypermetamorphosis A type of complete metamorphosis in which the different larval instars represent two or more different types of larvae (Figure 26–68).

hyperparasite A parasite whose host is another parasite.

hypodermis See **epidermis.**

hypognathous With the head and the mouthparts located ventrally (for example, as in Figure 2–13).

hypomeron In Coleoptera, the underside of the pronotum.

hypopharynx A median mouthpart structure anterior to the labium (Figures 2–16, 2–18 through 2–20, hyp); the ducts from the salivary glands are usually associated with the hypopharynx, and in some sucking insects the hypopharynx is the mouthpart structure containing the salivary channel.

hypopleural bristles A more or less vertical row of bristles on the hypopleuron, usually directly above the hind coxae (Diptera; Figure 34–6, hyb).

hypopleuron (pl., *hypopleura*) The lower part of the mesepimeron; a sclerite on the thorax located just above the hind coxae (Diptera; Figure 34–6, hypl).

hypostigmatic cell The cell immediately behind the point of fusion of Sc and R (Neuroptera, Myrmeleontoidea; Figure 27–4, hcl).

hypostomal bridge Mesal extension of the hypostomae on each side to meet below the foramen magnum.

hz Hertz (cycles per second).

ileum The anterior part of the hindgut (Figure 2–22, il).

imago (pl., *imagoes* or *imagines*) The adult or reproductive stage of an insect.

in-group The taxa that are the focus of interest in a phylogenetic study.

inclinate Bent toward the midline of the body.

indirect flight mechanism Generation of wing movements by means of muscles producing distortions in the shape of the thorax.

inferior appendage The lower one (Anisoptera) or two (Zygoptera) of the terminal abdominal appendages, used in grasping the female at the time of copulation (male Odonata; Figure 10–4A, ept; 10–4C, ppt).

infraepisternum A ventral subdivision of an episternum (Figure 10–4, iep).

inner vertical bristles The more mesally located of the large bristles on the vertex, between the ocelli and the compound eyes (Diptera; Figure 34–5, ivb).

inquiline An animal that lives in the nest or abode of another species.

instar The insect between successive molts, the first instar being between hatching and the first molt.

instinctive behavior Unlearned stereotyped behavior, in which the nerve pathways involved are hereditary.

integument The outer covering of the body.

interantennal suture A suture extending between the bases of the two antennae (Siphonaptera).

intercalary vein An extra longitudinal vein that develops from a thickened fold in the wing, more or less midway between two preexisting veins (Ephemeroptera; Figures 9–3, 9–4, 9–6, ICuA).

internuncial neuron (or *interneuron*) A neuron that connects with two (or more) other neurons.

intersternite An intersegmental sclerite on the ventral side of the thorax; the spinasternum.

interstitial Situated between two segments (interstitial trochanter of Coleoptera; Figure 26–9E, tr).

intestine Anterior portion of the hindgut, between the pyloric valve and the rectum.

intima The cuticular lining of the foregut, hindgut, and tracheae.

intra-alar bristles A row of two or three bristles situated on the mesonotum above the wing base, between the dorsocentral and the supra-alar bristles (Diptera; Figure 34–6, iab).

invagination An infolding or inpocketing.

isosmotic With an equal concentration of solutes.

iteroparous A type of life history in which the animal reproduces two or more times during its lifetime.

Johnston's organ A sense organ similar to a chordotonal organ, located in the second antennal segment of most insects; this organ functions in sound perception in some Diptera

joint An articulation of two successive segments or parts.

jugal lobe A lobe at the base of the wing, on the posterior side, proximad of the vannal lobe (Hymenoptera; Figure 28–13, 28–14, jl).

jugal vein The most posterior of the major longitudinal vein systems, according to Kukalová-Peck.

jugum A lobelike process at the base of the front wing, which overlaps the hind wing (Lepidoptera; Figure 30–5, j); a sclerite in the head (Hemiptera; Figures 2–17, 22–1, j).

katepleurite See **catapleurite.**

keeled With an elevated ridge or carina.

Khz Kilohertz (kilocycles per second).

kleptoparasite A parasite that feeds on food stored for the host larvae.

labellum The expanded tip of the labium (Diptera; Figures 2–19, 2–20, lbl).

labial Of or pertaining to the labium.

labial gland Exocrine organ opening on or at the base of the labium, usually functioning as salivary or silk gland.

labial palp One of a pair of small feelerlike structures arising from the labium (Figure 2–16C, lp).

labial suture The suture on the labium between the postmentum and prementum (Figure 2–16C, ls).

labium One of the mouthpart structures, the lower lip (Figures 2–13, lbm, 2–16C).

labrum The upper lip, lying just below the clypeus (Figure 2–13, lbr).

labrum-epipharynx A mouthpart representing the labrum and epipharynx.

lacinia (pl., *laciniae*) The inner lobe of the maxilla, borne by the stipes (Figure 2–16A, lc).

lamella (pl., *lamellae*) A leaflike plate.

lamellate With platelike structures or segments; lamellate antennae (Figures 2–15M, 26–6C,D).

lamina In the cuticle, a layer of cuticle with chitin microfibrils oriented in the same direction.

lamina lingualis (pl., *laminae linguales*) One of two median distal plates in the millipede gnathochilarium (Figure 5–30B, ll).

lanceolate Spear-shaped, tapering at each end.

larva (pl., *larvae*) The immature stage, between egg and pupa, of an insect having complete metamorphosis; the six-legged first instar of Acari (Figures 5–17B, 5–19A); an immature stage differing radically from the adult.

larviform Shaped like a larva.

laterad Toward the side, away from the midline of the body.

lateral Of or pertaining to the side (that is, the right or left side).

lateral oviduct A tube in the female internal genitalia connecting the ovaries and the common oviduct.

laterotergite A tergal sclerite located laterally or dorsolaterally.

lateroventral To the side (away from the midline of the body) and below.

leaf miner An insect that lives in and feeds on the leaf cells between the upper and lower surfaces of a leaf.

ligula The terminal lobe (or lobes) of the labium, the glossae and paraglossae.

linear Linelike, long and very narrow.

longitudinal Lengthwise of the body or of an appendage.

looper A caterpillar that moves by looping its body, that is, by placing the posterior part of the abdomen next to the thorax and then extending the anterior part of the body forward; a measuringworm.

lorum (pl., *lora*) The cheek; a sclerite on the side of the head (Hemiptera; Figures 22–1, 22–11, lo); the submentum in bees (Figure 28–6, smt).

luminescent Producing light.

lunule, frontal See frontal lunule.

maggot A vermiform larva; a legless larva without a well-developed head capsule (Diptera; Figure 2–43A).

Malpighian tubules Excretory tubes that arise near the anterior end of the hindgut and extend into the body cavity (Figure 2–22, mt).

mandible Jaw; one of the anterior pair of paired mouthpart structures (Figure 2–16D, md).

mandibulate With jaws fitted for chewing.

marginal cell A cell in the distal part of the wing bordering the costal margin (Diptera, Figure 34–4B, MC; Hymenoptera, Figure 28–3, MC).

marginal vein A vein on or just within the wing margin; the vein forming the posterior side of the marginal cell (Hymenoptera; Figures 28–3, 28–19B, mv).

margined With a sharp or keellike lateral edge.

maxilla (pl., *maxillae*) One of the paired mouthpart structures immediately posterior to the mandibles (Figure 2–16A, mx).

maxillary Of or pertaining to the maxilla.

maxillary palp A small feelerlike structure arising from the maxilla (Figure 2–16A, mxp).

maxilliped One of the appendages in Crustacea immediately posterior to the second maxillae.

mechanoreceptor A sensillum sensitive to physical displacement.

media The longitudinal vein between the radius and cubitus (Figure 2–10, M).

medial crossvein A crossvein connecting two branches of the media (Figure 2–10, m).

median In the middle; along the midline of the body.

mediocubital crossvein A crossvein connecting the media and cubitus (Figure 2–10, m-cu).

membrane A thin film of tissue, usually transparent; the part of the wing surface between the veins; the thin, apical part of a hemelytron (Hemiptera; Figure 22–4, mem).

membranous Like a membrane; thin and more or less transparent (wings); thin and pliable (cuticle).

mental setae Setae on the mentum (Odonata; Figure 10–3, mst).

mentum The distal part of the labium, which bears the palps and the ligula (Figure 2–16C, mn); a median, more or less triangular piece in the millipede gnathochilarium (Figure 5–30B, mn).

merocrine secretion Release of enzymes across the cell membrane, without destruction of the entire cell.

meroistic ovariole Ovariole with nurse cells.

meropleuron (pl., *meropleura*) A sclerite consisting of the meron (basal part) of the coxa and the lower part of the epimeron.

mesad Toward the midline of the body.

mesal At or near the midline of the body.

mesenteron The midgut, or middle portion of the alimentary tract (Figure 2–22, mg).

mesepimeron (pl. *mesepimera*) The epimeron of the mesothorax (Figures 2–6, 26–4, epm_2).

mesepisternum (pl., *mesepisterna*) The episternum of the mesothorax (Figures 2–6, 26–4, eps_2).

mesinfraepisternum A ventral subdivision of the mesepisternum (Odonata; Figure 10–4, iep_2).

meson The midline of the body, or an imaginary plane dividing the body into right and left halves.

mesonotum The dorsal sclerite of the mesothorax (Figure 2–1, n_2).

mesopleural bristles Bristles on the mesopleuron (Diptera; Figure 34–6, mpb).

mesopleuron (pl., *mesopleura*) The lateral sclerite(s) of the mesothorax; the upper part of the episternum of the mesothorax (Diptera; Figure 34–6, pl_2).

mesoscutellum The scutellum of the mesothorax (Figure 2–6, scl_2), usually simply called the *scutellum*.

mesoscutum The scutum of the mesothorax (Figure 2–6, sct_2).

mesosoma In Apocrita (Hymenoptera) the middle tagma of the body, consisting of the three thoracic segments and the first true abdominal segment (the propodeum).

mesosternum The sternum, or ventral sclerite, of the mesothorax.

mesothorax The middle or second segment of the thorax (Figure 2–1, th_2).

metamere A primary body segment (usually referring to the embryo).

metamorphosis A change in form during development.

metanotum The dorsal sclerite of the metathorax (Figure 2–1, n_3).

metascutellum The scutellum of the metathorax (Figure 2–6, scl_3).

metasoma In Apocrita (Hymenoptera) the posterior tagma of the body, consisting of all segments posterior to the propodeum.

metasternum The sternum, or ventral sclerite, of the metathorax.

metatarsus (pl., *metatarsi*) The basal segment of the tarsus (Figure 5–6).

metathorax The third or posterior segment of the thorax (Figure 2–1, th_3).

metazonite The posterior portion of a millipede tergum when the tergum is divided by a transverse groove.

metepimeron (pl., *metepimera*) The epimeron of the metathorax (Figure 2–6, epm_3).

metepisternum (pl., *metepisterna*) The episternum of the metathorax (Figure 2–6, eps_3).

metinfraepisternum A ventral subdivision of the metepisternum (Odonata; Figure 10–4, iep_3).

micropyle A minute opening (or openings) in the chorion of an insect egg, through which sperm enter the egg (Figure 2–37, mcp).

midgut The mesenteron, or middle portion of the alimentary tract (Figure 2–22, mg).

millimeter 0.001 meter, or 0.03937 inch (about 1/25 inch).

minute Very small; an insect a few millimeters in length or less would be considered minute.

molt A process of shedding the exoskeleton; ecdysis; to shed the exoskeleton.

molting gland See **prothoracic glands**.

monecious Having both male and female sex organs, hermaphroditic.

moniliform Beadlike, with rounded segments; moniliform antenna (Figure 2–15C).

monocondylic A joint with a single point of articulation.

monophyletic group A group that consists of an ancestral species and all of its descendants; recognized on the basis of shared derived characters (synapomorphies) among its members.

morphology The science of form or structure.

motor neuron A neuron that forms a synapse with a muscle.

mutualism The living together of two species of organisms with both species benefiting from the association.

myiasis A disease caused by the invasion of dipterous larvae.

myogenic Produced by muscle; contraction of a muscle generated by that muscle itself, without neuronal stimulus.

myriapod A many-legged arthropod; a centipede, millipede, pauropod, or symphylan.

naiad An aquatic, gill-breathing nymph.

nasute soldier (or nasutus) An individual of a termite caste in which the head narrows anteriorly into a snoutlike projection (Figure 19–2B).

neurogenic Produced by a neuron; contractions of muscle stimulated by a neuronal impulse.

nidi In the midgut, clusters of regenerative epithelial cells.

nocturnal Active at night.

node A knoblike or knotlike swelling.

nodiform In the form of a knob or knot.

nodus A strong crossvein near the middle of the costal border of the wing (Odonata; Figures 10–5 through 10–7, nod).

notal wing process Point at which the notum articulates with the wing (or axillary sclerites at the base of the wing).

notaulus (pl., *notauli*) A longitudinal line on the mesoscutum of Hymenoptera, marking the separation of the dorsal longitudinal and dorsoventral flight muscles (Figure 28–4A, nt); also sometimes called *notaulix* (pl., *notaulices*), *parapsidal furrow*, or *parapsidal suture*.

notopleural bristles Bristles on the notopleuron (Diptera; Figure 34–6, nb).

notopleural suture A suture between the notum and the pleural sclerites (Figure 26–4, npls).

notopleuron (pl., *notopleura*) An area on the thoracic dorsum, at the lateral end of the transverse suture (Diptera; Figure 34–6, npl).

notum (pl., *nota*) The dorsal sclerite of a thoracic segment; the fused second gonapophyses of the ovipositor.

nurse cells Nutritive cells associated with the developing oocyte.

nymph An immature stage (following hatching) of an insect that does not have a pupal stage; the immature stage of Acari that has eight legs.

oblique vein A slanting crossvein; in Odonata, where Rs crosses M_{1+2} (Figure 10–5, obv).

obtect pupa A pupa in which the appendages are more or less glued to the body surface, as in the Lepidoptera (Figures 2–44A,B, 30–4).

occipital foramen See **foramen magnum**.

occipital suture (or *occipital sulcus*) A transverse suture in the posterior part of the head that separates the vertex from the occiput dorsally and the genae from the postgenae laterally (Figure 2–13, os).

occiput The dorsal posterior part of the head, between the occipital and postoccipital sutures (Figure 2–13, ocp).

ocellar bristles Bristles arising close to the ocelli (Diptera; Figure 34–5, ob).

ocellar triangle A slightly raised triangular area in which the ocelli are located (Diptera; Figure 34–5, ot).

ocellus (pl., *ocelli*) A simple eye of an insect or other arthropod (Figure 2–13, oc).

olfaction The sense of smell; the ability to detect chemicals in a gas.

olistheter A tongue-in-groove mechanism connecting the first and second gonapophyses of the ovipositor.

ommatidium (pl., *ommatidia*) A single unit or visual section of a compound eye (Figure 2–29D).

onisciform larva See platyform larva.

oocyte Egg.

oogenesis The production of eggs.

oogonium (pl., *oogonia*) The primary germ cells of the female.

ootheca (pl., *oothecae*) The covering or case of an egg mass (Mantodea, Blattodea).

open cell A wing cell extending to the wing margin, not entirely surrounded by veins.

open coxal cavity One bounded posteriorly by a sclerite of the next segment (front coxl cavities, Coleoptera; Figure 26–7A), or one touched by one or more pleural sclerites (middle coxal cavities, Coleoptera; Figure 26–7C).

operculumn (pl., *opercula*) A lid or cover.

opisthognathous With the mouthparts directed backward.

opisthorhynchous With the beak directed backward.

oral Pertaining to the mouth.

oral vibrissae A pair of stout bristles, one on each side of the face near or just above the oral margin, and larger than the other bristles on the vibrissal ridge (Diptera; Figure 34–5, ov).

orbital plate See genovertical plate.

order A subdivision of a class or subclass, containing a group of related superfamilies or families.

osmeterium (pl., *osmeteria*) A fleshy, tubular, eversible, usually Y-shaped gland at the anterior end of certain caterpillars (Papilionidae; Figure 30–3, osm).

ostiole A small opening.

ostium (pl., *ostia*) A slitlike opening in the insect heart.

out-group In a phylogenetic study, taxa outside of the focus of interest; used to hypothesize the polarity of character states (that is, ancestral or derived) found in the in-group. The state found in the out-group is hypothesized to be the ancestral, or plesiomorphic, state.

outer vertical bristles The more laterally located of the large bristles on the vertex, between the ocelli and the compound eyes (Diptera; Figure 34–5, ovb).

ovariole A more or less tubular division of an ovary (Figure 2–31, ovl).

ovary The egg-producing organ of the female (Figures 2–22, 2–31A, ovy).

oviduct The tube leading away from the ovary through which the eggs pass (Figures 2–22, 2–31A, ovd).

oviparous Laying eggs.

ovipore The external opening of the female reproductive system through which the eggs pass during oviposition.

oviposit To lay or deposit eggs.

ovipositor The egg-laying apparatus; the external genitalia of the female (Figures 2–1, 2–32, 10–4E, and 28–5, ovp).

oviscapt Modification of the terminal abdominal segments of a female to serve as an egg-laying organ.

paedogenesis The production of eggs or young by an immature or larval stage of an animal.

palp A segmented process born by the maxillae or labium (Figure 2–16, lp, mxp); the pedipalp of a spider.

palpifer The lobe of the maxillary stipes that bears the palp (Figure 2–16A, plf).

palpiger The lobe of the mentum of the labium that bears the palp (Figure 2–16C, plg).

panoistic ovariole Ovariole without nurse cells.

papilla A small nipplelike elevation.

paracymbium An appendage arising from the cymbium of the pedipalp of a male spider.

paraglossa (pl., *paraglossae*) One of a pair of lobes at the apex of the labium, laterad of the glossae (Figure 2–16C, pgl).

paramere A structure in the male genitalia of insect, usually a lobe or process at the base of the aedeagus.

paranotum Lateral expansion of the notum.

paraphyletic group A group of species, derived from a common ancestor but not including all of its descendants; recognized on the basis of shared ancestral character states (symplesiomorphies).

paraproct One of a pair of lobes bordering the anus lateroventrally (Figures 2–1 and 10–4A, ppt).

parasite An animal that lives in or on the body of another living animal (its host), at least during a part of its life cycle, feeding on the tissues of its host; most entomophagous insect parasites kill their host (see also **parasitoid**).

parasitic Living as a parasite.

parasitoid An animal that feeds in or on another living animal for a relatively long time, consuming all or most of its tissues and eventually killing it (also used as an adjective, describing this mode of life). Parasitoid insects in this book are referred to as *parasites*.

parsimony, principle of In a scientific context, the assumption that the simplest explanation of the data observed is the best hypothesis.

parthenogenesis Development of the egg without fertilization.

patella A leg segment between the femur and tibia (arachnids; Figure 5–6).

paurometabolous With simple metamorphosis, the young and adults living in the same habitat, and the adults winged.

pecten A comblike or rakelike structure.

pectinate With branches or processes like the teeth of a comb; pectinate antenna (Figure 2–15H); pectinate tarsal claw (Figure 26–11B).

pedicel The second segment of the antenna (Figure 2–15N, ped); the stem of the abdomen, between the thorax and the gaster (ants).

pedipalps The second pair of appendages of an arachnid (Figure 5–6, palp; 5–12).

pelagic Inhabiting the open sea; ocean-dwelling.

penultimate Next to the last.

pericardial sinus The body cavity surrounding the dorsal blood vessel, limited ventrally by the dorsal diaphragm.

perineural sinus The body cavity surrounding the ventral nerve cord, limited dorsally by the ventral diaphragm.

peristalsis Waves of contraction.

peristome The ventral margin of the head, bordering the mouth.

peritrophic membrane A membrane in insects secreted by the cells lining the midgut; this membrane is secreted when food is present and forms an envelope around the food; it usually pulls loose from the midgut, remains around the food, and passes out with the feces.

perivisceral sinus The body cavity surrounding the digestive system, reproductive system, etc., between the dorsal and ventral diaphragms.

petiolate Attached by a narrow stalk or stem.

petiole A stalk or stem; the narrow stalk or stem by which the metasoma is attached to the mesosoma (Hymenoptera); in ants, the nodelike first segment of the metasoma.

pH A measure of the acidity or alkalinity of a medium. A pH value of 7.0 indicates neutral; lower values indicate acid, and higher values alkaline. Defined as $-\log [H^+]$.

phallotreme External opening of the male reproductive system on the aedeagus.

phallus The male copulatory organ, including any processes that may be present at its base.

pharynx The anterior part of the foregut, between the mouth and the esophagus (Figure 2–22, phx).

pheromone A substance given off by one individual that causes a specific reaction by other individuals of the same species, such as sex attractants, alarm substances, etc.

photoperiod The relative amount of time during the day in which it is light (or dark).

phragma (pl., *phragmata*) A platelike apodeme or invagination of the dorsal wall of the thorax (Figure 2–7, ph).

phylogenetics School of systematics that seeks to recognize monophyletic groups on the basis of shared derived characters.

phylum (pl., *phyla*) One of the major divisions of the animal kingdom.

phytophagous Feeding on plant.

pictured With spots or bands (pictured wings; Figure 34–77).

pilifer One of a pair of lateral projections on the labrum (Lepidoptera; Figure 30–2, pf).

pilose Covered with hair.

planidium larva A type of first-instar larva in certain Diptera and Hymenoptera that undergoes hypermetamorphosis; a larva that is legless and somewhat flattened.

plastron A bed of very dense and very fine hairs used to hold an air bubble close to the body and across which gas exchange takes place.

platyform larva A larva that is extremely flattened, as the larva of Psephenidae (Figure 26–44) (also called *onisciform larva*).

plesiomorphy The ancestral state of a character.

pleural Pertaining to the pleura, or lateral sclerites of the body; lateral.

pleural apophysis (or arm) Internal process extending from the pleural suture to the sternal apophyses.

pleural suture (or sulcus) A suture of a thoracic pleuron extending from the base of the wing to the base of the coxa, which separates the episternum and epimeron (Figures 2–1, 2–6, pls).

pleural wing process The structure articulating with the wing (specifically with the second axillary sclerite).

pleurite A lateral or pleural sclerite.

pleuron (pl., *pleura*) The lateral area of a segment.

pleuropodium (pl., *pleuropodia*) Embryonic appendages of the first abdominal segment.

pleurotergite A sclerite containing both pleural and tergal elements.

plumose Featherlike; plumose antenna (Figure 2–15I).

poikilothermous Cold-blooded, the body temperature rising or falling with the environmental temperature.

point A small triangle of stiff paper, used in mounting small insects (Figure 35–13).

pollen basket See **corbicula**.

pollen rake A comblike row of bristles at the apex of the hind tibia of a bee (Figure 28–66, pr).

polyembryony An egg developing into two or more embryos.

polyphyletic group A group of species that do not share a common ancestor; such an unnatural group is usually proposed on the basis of characters that represent parallel or convergent characters (homoplasies).

polytomy On a cladogram a node that gives rise to more than two branches.

polytrophic ovariole Meroistic ovariole in which trophocytes pass into the vitellarium with the oocyte.

porrect Extending forward horizontally; porrect antennae (Figure 34–23G,I).

postabdomen The modified posterior segments of the abdomen, which are usually more slender than the anterior segments (Crustacea, Figure 5–24A, pa; see also the postabdomen in a scorpion, Figure 5–3).

postalar callus A rounded swelling on each side of the mesonotum, between the base of the wing and the scutellum (Diptera; Figure 34–6, pc).

posterior Hind or rear.

posterior cell One of the cells extending to the hind margin of the wing, between the third and sixth longitudinal veins (Diptera; Figure 34–4B, P).

posterior crossvein A crossvein at the apex of the discal cell (Diptera; Figure 34–4B, pcv).

postgena (pl., *postgenae*) A sclerite on the posterior lateral surface of the head, posterior to the gena (Figure 2–13, pg).

postgenal bridge Mesal extension of the postgenae on each side to meet below the foramen magnum.

posthumeral bristles Bristles on the anterolateral surface of the mesonotum, just posterior to the humeral callus (Diptera; Figure 34–6 pb).

postmarginal vein The vein along the anterior margin of the front wing, beyond the point where the stigmal vein arises (Hymenoptera; Figure 28–19B, pm).

postmentum The basal portion of the labium, proximad of the labial suture (Figure 2–16C, pmt).

postnodal crossveins: A series of crossveins just behind the costal margin of the wing, between the nodus and stigma, and extending from the costal margin of the wing to R_1 (Odonata; Figures 10–5, 10–6, pn).

postnotum (pl., *postnota*) A notal plate behind the scutellum bearing a phragma, often present in wing-bearing segments (Figure 2–6, PN).

postoccipital suture The transverse suture on the head immediately posterior to the occipital suture (Figure 2–13, pos).

postocciput The extreme posterior rim of the head, between the postoccipital suture and the foramen magnum (Figure 2–13, po).

postpetiole The second segment of a two-segmented pedicel (ants).

postscutellum A small transverse piece of a thoracic notum immediately behind the scutellum; in Diptera, an area immediately behind or below the mesoscutellum (Figure 34–13B, pscl).

postvertical bristles A pair of bristles behind the ocelli, usually situated on the posterior surface of the head (Diptera; Figure 34–5, pv).

preapical Situated just before the apex; preapical tibial bristles of Diptera (Figure 34–26B, ptbr).

prebasilare A narrow transverse sclerite, just basal to the mentum in the gnathochilarium of some millipedes (Figure 5–30B, pbs).

precosta The most anterior of the major longitudinal wing veins, according to Kukalová-Peck.

predaceous Feeding as a predator.

predator An animal that attacks and feeds on other animals (its prey), usually animals smaller or less powerful than itself. The prey is usually killed and mostly or entirely eaten; each predator eats many prey individuals.

prefemur The second trochanter segment of the leg.

pregenital Anterior to the genital segments of the abdomen.

prementum The distal part of the labium, distad of the labial suture, on which all the labial muscles have their insertions (Figure 2–16C, prmt).

preoral Anterior to or in front of the mouth.

prepectus An area along the anteroventral margin of the mesepisternum, set off by a suture (Hymenoptera; Figure 28–4, pp).

prepupa A quiescent stage between the larval period and the pupal period; the third instar of a thrips (Figure 23–2B).

presutural bristles Bristles on the mesonotum immediately anterior to the transverse suture and adjacent to the notopleuron (Diptera; Figure 34–6, psb).

pretarsus (pl., *pretarsi*) The terminal segment of the leg, typically consisting of a pair of claws and one or more padlike structures (Figure 2–8B–D, ptar).

proboscis Collectively, the extended, beaklike mouthparts (Figure 34–36, prb).

proclinate Inclined forward or downward.

proctodaeum The hindgut, or the hindmost of the three major divisions of the alimentary tract, from the Malpighian tubules to the anus.

procurved A line connecting a row of eyes in a spider in which the ends of the line are anterior to the center of the line.

procuticle The form in which the cuticle is initially secreted by the epidermis, before sclerotization takes place.

produced Extended, prolonged, or projecting.

proepimeron (pl., *proepimera*) The epimeron of the prothorax (Figure 26–4, epm_1).

proepisternum (pl., *proepisterna*) The episternum of the prothorax (Figure 26–4, eps_1).

profile The outline as seen from the side or in lateral view.

prognathous Having the head horizontal and the mouthparts projecting forward.

proleg One of the fleshy abdominal legs of certain insect larvae (Figure 30–3, prl).

prominence A raised, produced, or projecting portion.

prominent Raised, produced, or projecting.

promote To move anteriorly.

pronate To turn the leading edge of the wing downward.

pronotal comb A row of strong spines borne on the posterior margin of the pronotum (Siphonaptera; Figures 31–1, 31–2A).

pronotum The dorsal sclerite of the prothorax (Figures 2–1, 2–6, n_1).

propleural bristles Bristles located on the propleuron (Diptera; Figure 34–6, ppb).

propleuron (pl., *propleura*) The lateral portion, or pleuron, of the prothorax (Figure 34–6, pl_1).

propodeum The posterior portion of the mesosoma, which is actually the first abdominal segment united with the thorax (Hymenoptera, suborder Apocrita; Figure 28–4, prd).

proprioception Detection by an animal of the position of parts of its own body.

prosoma The anterior part of the body, usually the cephalothorax; the anterior part of the head or cephalothorax.

prosternum The sternum, or ventral sclerite, of the prothorax.

prothoracic glands Endocrine glands located in the prothorax (generally) that secrete ecdysone.

prothoracicotropic hormone See **brain hormone.**

prothorax The anterior of the three thoracic segments (Figure 2–1, th_1).

protocerebrum The dorsal lobes of the brain, innervating (inter alia) the compound eyes and ocelli.

protonymph The second instar of a mite (Figure 5–17C).

proventriculus The valve between the foregut and midgut.

proximad Toward the end or portion nearest the body.

proximal Nearer to the body or to the base of an appendage.

prozonite The anterior portion of a millipede tergum when the tergum is divided by a transverse groove.

pruinose Covered with a waxy, whitish powder.

pseudarolium (pl., *pseudarolia*) A pad at the apex of the tarsus resembling an arolium.

pseudocellus Circular areas of thin, corrugated cuticle on the head and body of Collembola.

pseudocercus (pl., *pseudocerci*) See **urogomphi.**

pseudocubitus A vein appearing as the cubitus, but actually formed by the fusion of the branches of M and Cu_1 (Neuroptera; Figure 27–3B, pscu).

pseudomedia A vein appearing as the media, but actually formed by the fusion of branches of Rs (Neuroptera; Figure 27–3B, psm).

pseudopupa A coarctate larva; a larva in a quiescent pupalike condition, one or two instars before the true pupal stage (Coleoptera, Meloidae; Figure 26–68H).

pseudovipositor See oviscapt.

pteralia See axillary sclerites.

pteropleural bristles Bristles on the pteropleuron (Diptera; Figure 34–6, ptb).

pteropleuron (pl., *pteropleura*) A sclerite on the side of the thorax, just below the base of the wing, and consisting of the upper part of the mesepimeron (Diptera; Figure 34–6, pt).

pterostigma A thickened opaque spot along the costal margin of the wing, near the wing tip (see also stigma) (Odonata; Figures 10–5, 10–6, st).

pterothorax The wing-bearing segments of the thorax (mesothorax and metathorax).

pterygote Winged; a member of the subclass Pterygota.

ptilinum A temporary bladderlike structure that can be inflated and thrust out through the frontal (or ptilinal) suture, just above the bases of the antennae, at the time of emergence from the puparium (Diptera).

PTTH See brain hormone.

pubescent Downy, covered with short fine hairs.

pulvilliform Lobelike or padlike; shaped like a pulvillus; pulvilliform empodium (Figure 34–2B, emp).

pulvillus (pl., *pulvilli*) A pad or lobe beneath each tarsal claw (Diptera; Figure 34–2, pul).

punctate Pitted or beset with punctures.

puncture A tiny pit or depression.

pupa (pl., *pupae*) The stage between the larva and the adult in insects with complete metamorphosis, a nonfeeding and usually an inactive stage (Figure 2–44).

puparium (pl., *puparia*) A case formed by the hardening of the last larval skin, in which the pupa is formed (Diptera; Figure 2–44F).

pupate To transform to a pupa.

pupiparous Giving birth to larvae that are full grown and ready to pupate.

pygidium The last dorsal segment of the abdomen.

pyloric valve The valve between the midgut and hindgut.

quadrangle A cell immediately beyond the arculus (Odonata, Zygoptera; Figure 10–6F, G, q).

quadrate Four-sided.

radial cell A cell bordered anteriorly by a branch of the radius; the marginal cell (Hymenoptera; Figure 28–3, MC).

radial crossvein A crossvein connecting R_1 and the branch of the radius immediately behind it (Figure 2–10, r).

radial sector The posterior of the two main branches of the radius (Figure 2–10, Rs).

radius The longitudinal vein between the subcosta and the media (Figure 2–10, R).

raptorial Fitted for grasping prey; raptorial front legs (Figure 22–2).

reclinate Inclined backward or upward.

rectum The posterior region of the hindgut (Figure 2–22, rec).

recurrent vein One of two transverse veins immediately posterior to the cubital vein (Hymenoptera; Figure 28–3, rv); a vein at the base of the wing between the costa and the subcosta, extending obliquely from the subcosta to the costa (Neuroptera; Figure 27–2C, hv).

recurved Curved upward or backward; in spiders, a line connecting a row of eyes in which the ends are posterior to the middle of the line.

relationship In phylogenetic systematics (cladistics), the relative recency of common ancestry.

remote To move posteriorly.

reniform Kidney-shaped.

reticulate Like a network.

retina The receptive apparatus of an eye.

retractile Capable of being pushed out and drawn back in.

rhabdom A rodlike light-sensitive structure formed of the inner surfaces of adjacent sensory cells in the ommatidium of a compound eye (Figure 2–29, rh).

Riker mount A thin glass-topped exhibition case filled with cotton batting (Figure 35–20).

rostrum Beak or snout.

rudimentary Reduced in size, poorly developed, embryonic.

rugose Wrinkled.

saprophagous Feeding on dead or decaying plant or animal materials, such as carrion, dung, dead logs, etc.

scape The basal segment of an antenna (Figure 2–15N, scp).

scapula (pl., *scapulae*) One of two sclerites on the mesonotum immediately lateral of the notauli (Hymenoptera; Figure 28–4, sca); also called parapsis.

scarabaeiform larva A grublike larva, that is, one with the body thickened and cylindrical, with a well-developed head and thoracic legs, without prolegs, and usually sluggish (Figures 2-43B, 26–31).

scavenger An animal that feeds on dead plants or animals, or decaying materials, or on animal wastes.

scent gland A gland producing an odorous substance.

scientific name A latinized name, internationally recognized, of a species or subspecies. The scientific name of a species consists of the generic and specific names, and that of a subspecies consists of the generic, specific, and subspecific names. Scientific names are always printed in italics.

sclerite A hardened body-wall plate bounded by sutures or membranous areas.

sclerotization The process of becoming hardened.

sclerotized Hardened.

scolopophorous organ See campaniform sensillum.

scolytoid larva A fleshy larva resembling the larva of a scolytid beetle.

scopa (pl., *scopae*) A small, dense tuft of hair.

scraper The sharpened anal angle of the front wing (tegmen) of a cricket or katydid, a part of the stridulating mechanism.

scrobe A groove or furrow; antennal scrobe (Figures 26–3, 26–88A, G, agr).

scutellum A sclerite of the thoracic notum (Figure 2–6, scl); the mesoscutellum, appearing as a more or less triangular sclerite behind the pronotum (Hemiptera, Coleoptera).

scutum The middle division of a thoracic notum, just anterior to the scutellum (Figure 2–6, sct).

sebaceous glands Glands secreting fatty or oily material.

secondary segmentation Subdivision of the body of arthropods in which the externally visible sclerites and membranes do not correspond to the internal attachment of longitudinal muscle.

sectorial crossvein A crossvein connecting two branches of the radial sector (Figure 2–10, s).

segment A subdivision of the body or of an appendage, between joints or articulations.

segmented antenna An antenna composed of more than three true, musculated segments; limited to Diplura and Collembola.

semiaquatic Living in wet places or partially in water.

seminal vesicle A structure, usually saclike, in which the seminal fluid of the male is stored before being discharged; usually an enlargement of the vas deferens (Figure 2–31B, smv).

sense cone or sense peg A minute cone or peg, sensory in function (Figures 2–27, 23–5, scn).

sensillum (pl., *sensilla*) An organ capable of detecting external stimuli.

sensory neuron A neuron capable of generating an action potential in response to an external stimulus (such as physical displacement, temperature, humidity, chemicals, etc.).

serrate Toothed along the edge like a saw; serrate antenna (Figure 2–15G).

serrula Sawlike anterior margin of the basal endite segment on the spider pedipalp.

sessile Attached or fastened, incapable of moving from place to place; attached directly, without a stem or petiole.

seta (pl., *setae*) A bristle.

setaceous Bristlelike; setaceous antenna (Figure 2–15A).

setate Provided with bristles.

setulose Bearing short, blunt bristles.

sigmoid Shaped like the letter S.

simple Unmodified, not complicated; not forked, toothed, branched, or divided.

sister groups On a cladogram, the two taxa (or groups of taxa) that arise from a single node. Sister groups are each others' closest relatives.

spatulate Spoon-shaped; broad apically and narrowed basally, and flattened.

species A group of individuals or populations that are similar in structure and physiology and can interbreed and produce fertile offspring, and that differ in structure and/or physiology from other such groups and normally do not interbreed with them.

sperm duct A tube connecting the bursa copulatrix of ditrysian Lepidoptera to the vagina.

sperm follicle A tubelike subdivision of the testis in which spermatogenesis occurs.

spermatheca (pl., *spermathecae*) A saclike structure in the female in which sperm from the male are received and often stored (Figure 2–31A, spth).

spermatogenesis The production of sperm cells.

spermatogonium A primary germ cell of the male.

spermatophore A capsule containing sperm, produced by the males of some insects.

spermatozoon (pl., *spermatozoa*) Functional, usually motile, sperm cell.

spinasternum An intersegmental sclerite of the thoracic venter that bears a median apodeme or spina, associated with or united with the sclerite immediately anterior to it; also called the *intersternite*.

spindle-shaped Elongate and cylindrical, thickened in the middle and tapering at the ends.

spine A thornlike outgrowth of the cuticle.

spinneret A structure with which silk is spun, usually fingerlike in shape (Figures 5–6, 5–8).

spinose Beset with spines; spinose costa in Diptera (Figure 34–22H).

spiracle An external opening of the tracheal system; a breathing pore (Figures 2–1, 2–25, spr).

spiracular bristles Bristles very close to a spiracle (Diptera; Figure 34–25, spbr).

spiracular plate A platelike sclerite next to or surrounding the spiracle.

spur A movable spine (when on a leg segment, usually located at the apex of the segment).

spurious claw A false claw; a stout bristle that looks like a claw (spiders).

spurious vein A veinlike thickening of the wing membrane between two true veins; an adventitious longitudinal vein between the radius and the media, crossing the r-m crossvein (Diptera, Syrphidae; Figure 34–15A–C, spv).

squama (pl., *squamae*) A scalelike structure; a calypter; the palpiger (Odonata; Figure 10–9, plg).

stadium (pl., *stadia*) The period between molts in a developing arthropod.

stalked With a stalk or stem; with a narrow, stemlike base; of veins, fused together to form a single vein.

stemmata (sing., *stemma*) The lateral eyes of insect larvae.

sternacostal suture (or sulcus) A suture of the thoracic sternum, the external mark of the sternal apophysis or furca, separating the basisternum from the sternellum.

sternal apophysis (or sternal arm) See furca.

sternellum The part of the eusternum posterior to the sternacostal suture (sulcus).

sternite A subdivision of a sternum; the ventral plate of an abdominal segment.

sternopleural bristles Bristles on the sternopleuron (Diptera; Figure 34–6, stb).

sternopleuron (pl., *sternopleura*) A sclerite in the lateral wall of the thorax, just above the base of the middle leg (Diptera; Figure 34–6, stpl).

sternum (pl., *sterna*) A sclerite on the ventral side of the body; the ventral sclerite of an abdominal segment (Figure 2–1, stn).

stigma (pl., *stigmata*) A thickening of the wing membrane along the costal border near the apex (Figures 10–5, 10–6, 28–1, st).

stigmal vein A short vein extending posteriorly from the costal margin of the wing, usually a little beyond the middle of the wing (Hymenoptera; Figure 28–19B, sv).

stipes (pl., *stipites*) The second segment or division of a maxilla, which bears the palp, the galea, and the lacinia (Figure 2–16A, stp); lateral lobes of the millipede gnathochilarium (Figure 5–30B, stp).

stomadaeum The foregut.

storage excretion The removal of metabolic wastes by isolation within certain tissues or cells.

stria (pl., *striae*) A groove or depressed line.

striate With grooves or depressed lines.

stridulate To make a noise by rubbing two structures or surfaces together.

stripe A longitudinal color marking.

stylate With a style; stylelike; stylate antenna (Figure 2–15K).

style A bristlelike process at the apex of an antenna (Figure 2–15K, sty); a short slender, fingerlike process (Figure 8–1, sty).

stylet A needlelike structure; one of the piercing structures in sucking mouthparts.

stylus (pl., *styli*) A short, slender, fingerlike process (Figure 8–1, sty).

subalare (or subalar sclerite) An epipleurite located posterior to the pleural wing process.

subantennal sulcus A groove on the face extending ventrally from the base of the antenna (Figures 2–13, 28–17, sas).

subapical Located just proximad of the apex.

subbasal Located just distad of the base.

subclass A major subdivision of a class, containing a group of related orders.

subcosta The longitudinal vein between the costa and the radius (Figure 2–10, Sc).

subcoxa Leg segment of primitive arthropods basad of the coxa, hypothesized to be incorporated into the thoracic wall to form the thoracic pleurites (see also **anapleurite**, **catapleurite**).

subequal Approximately equal in size or length.

subesophageal ganglion The knotlike swelling at the anterior end of the ventral nerve cord, usually just below the esophagus (Figures 2–22, 2–26, segn).

subfamily A major division of a family, containing a group of related tribes or genera. Subfamily names end in *-inae*.

subgenal suture (or sulcus) The horizontal suture below the gena, just above the bases of the mandibles and maxillae, a lateral extension of the epistomal suture (Figure 2–13, sgs).

subgenital plate A platelike sternite that underlies the genitalia.

subgenus (pl., *subgenera*) A major subdivision of a genus, containing a group of related species. In scientific names, subgeneric names are capitalized and placed in parentheses following the genus name.

subimago The first of two winged instars of a mayfly after it emerges from the water.

submarginal cell One or more cells lying immediately behind the marginal cell (Hymenoptera; Figure 28–3, SM).

submarginal vein Vein immediately behind and paralleling the costal margin of the wing (Hymenoptera; Figure 28–19B, sm).

submentum The basal part of the labium (Figure 2–16C, smt).

subocular suture (or *subocular sulcus*) A suture extending ventrally from the compound eye (Figure 2–13, sos).

suborder A major subdivision of an order, containing a group of related superfamilies or families.

subquadrangle A cell immediately behind the quadrangle (Odonata, Zygoptera; Figure 10–6, sq).

subspecies A subdivision of a species, usually a geographic race. The different subspecies of a species ordinarily are not sharply differentiated. They intergrade with one another and are capable of interbreeding. (For names of subspecies, see scientific name.)

subtriangle A cell or group of cells proximad of the triangle (Odonata, Anisoptera; Figure 10–5, str).

successions Groups of species that successively occupy a given habitat as the conditions of the habitat change.

sulcate With a groove or furrow.

sulcus (pl., *sulci*) A groove formed by an infolding of the body wall (Figure 2–4); a groove or furrow.

superfamily A group of closely related families. Superfamily names end in *-oidea*.

superior appendage One of the two upper appendages at the end of the abdomen, a cercus (Odonata; Figure 10–4, cr).

supinate To turn the trailing edge of the wing downward.

supplement An adventitious vein formed by a number of crossveins being lined up to form a continuous vein, located behind and more or less parallel to one of the main longitudinal veins (Odonata; Figure 10–5, mspl, rspl).

supra-alar bristles A longitudinal row of bristles on the lateral portion of the mesonotum, immediately above the wing base (Diptera; Figure 34–6, spb).

suture An external, linelike groove in the body wall, or a narrow, membranous area between sclerites (Figure 2–4, su); the boundary between two fused sclerites; the line of juncture of the elytra (Coleoptera).

swimmeret An abdominal appendage that functions as a swimming organ (Crustacea; Figure 5–22, sw).

symbiont An organism living in symbiosis with another organism.

symbiosis The living together of two species, in a more or less intimate association, benefiting both.

symmetry A definite pattern of body organization; bilateral symmetry, a type of body organization in which the various parts are arranged more or less symmetrically on either side of a median vertical plane, that is, where the right and left sides of the body are essentially similar.

symplesiomorphy A shared, ancestral character state among taxa.

synapomorphy A shared, derived character state among taxa; used as the basis for recognizing monophyletic groups.

synchronous muscle A muscle in which each contraction is initiated by the reception of a neuronal impulse.

synonyms Two or more names for the same thing (taxon).

systematics The study of the relationships among organisms.

taenidium (pl., *taenidia*) A circular or spiral thickening in the inner wall of a trachea.

tagma (pl., *tagamata*) A group of segments of the body specialized for a given function; e.g., the head, thorax, and abdomen of insects.

tandem One behind the other, the two connected or attached together.

tarsal claw A claw at the apex of the tarsus, derived from the pretarsal segment of the leg (Figure 2–8, tcl).

tarsal formula The number of tarsal segments on the front, middle, and hind tarsi, respectively.

tarsomere A subdivision, or "segment," of the tarsus.

tarsus (pl., *tarsi*) The leg segment immediately beyond the tibia, sometimes consisting of one or more "segments" or subdivisions (Figure 2–8, ts).

taxon (pl., *taxa*) A group of organisms classified together.

taxonomy The science of classification into categories of varying rank, and the describing and naming of these categories.

tegmen (pl., *tegmina*) The thickened or leathery front wing of an orthopteran.

tegula (pl., *tegulae*) A small, scalelike structure overlying the base of the front wing (Figure 28–4, tg).

telopod (telopodite) The portion of the leg beyond the coxopodite.

telotrophic ovariole Meroistic ovariole in which the nurse cells remain in the germarium.

telson The posterior part of the last abdominal segment (Crustacea); the posterior spinelike tail of the Xiphosura; the posterior nonmetameric portion of the body.

tenaculum A minute structure on the ventral side of the third abdominal segment that serves as a clasp for the furcula (Collembola).

teneral A term applied to recently molted, pale, soft-bodied individuals.

tentorial bridge A transverse, internal sclerotized bar that unites the tentorial arms and braces the head.

tentorial pits Pitlike depressions on the surface of the head that mark the points of union of the arms of the tentorium with the outer wall of the head. There are usually two tentorial pits in the epistomal suture (Figure 2–13, 2–14, atp) and one at the lower end of each postoccipital suture (Figure 2–13, 2–14, ptp).

tentorium The endoskeleton of the head, usually consisting of two pairs of apodemes (Figure 2–14).

tergite A subdivision of the tergum.

tergosternal muscles One of the primary sets of segmental muscles inserted on the tergum dorsally and the sternum ventrally, in pterothoracic segments contraction results in depression of the notum and contributes significantly to elevation of the wings.

tergum (pl., *terga*) A sclerite on the dorsal side of the body; the dorsal sclerite of an abdominal segment (Figure 2–1, t).

terminal At the end; at the posterior end (of the abdomen); the last of a series.

terrestrial Living on land.

testis (pl., *testes*) The sex organ in the male that produces sperm (Figure 2–31B, tst).

thelytoky A form of parthenogenesis in which only females are produced from unfertilized eggs, males being very rare or absent.

thorax The body region behind the head, which bears the legs and wings (Figure 2–1, th).

tibia (pl., *tibiae*) The fourth segment of the leg, between the femur and the tarsus (Figure 2–8, tb).

tibial spur A large spine on the tibia, usually located at the distal end of the tibia.

tormogen cell An epidermal cell associated with a seta, which forms the setal membrane or socket (Figure 2–2, tmg).

toxicognath A poison jaw (centipedes, Figure 5–32, pj; a modified leg).

trachea (pl., *tracheae*) A tube of the respiratory system, lined with taenidia, ending externally at a spiracle, and terminating internally in the tracheoles (Figure 2–25).

tracheole The fine terminal branch of the respiratory tubes.

translucent Allowing light to pass through, but not necessarily transparent.

transverse Across, at right angles to the longitudinal axis.

transverse suture A suture across the mesonotum (Diptera; Figure 34–6, trs).

triangle A small triangular cell or group of cells near the base of the wing (Odonata, Anisoptera; Figures 10–5, 10–7, tri).

tribe A subdivision of a subfamily, containing a group of related genera. Names of tribes end in *-ini*.

trichobothria Minute sensory hairs on the tarsi (spiders; Figure 5–7C, TR).

trichogen cell The epidermal cell from which a seta develops (Figure 2–27, trg).

tripectinate Having three rows of comblike branches.

tritocerebrum The ventral lobes of the brain.

triungulin larva The active first-instar larva of the Strepsiptera and certain beetles that undergo hypermetamorphosis (Figure 26–68A, 32–1F).

trochanter The second segment of the leg, between the coxa and the femur (Figure 2–8, tr).

trochantin A small sclerite in the thoracic wall immediately anterior to the base of the coxa (Figure 26–9B, tn).

trophallaxis The exchange of alimentary canal liquid among colony members of social insects and guest organisms, either mutually or unilaterally; trophallaxis may be stomodeal (from the mouth) or proctodeal (from the anus).

trophocyte See **nurse cells**.

tropism The orientation of an animal with respect to a stimulus, either positive (turning toward the stimulus) or negative (turning away from the stimulus).

truncate Cut off square at the end.

truss cell See **hypostigmatic cell**.

tubercle A small knotlike or rounded protuberance.

tylus The clypeal region of the head (Hemiptera; Figure 22–1, ty).

tymbal A sclerotized plate in the sound-producing organ of a cicada (Figure 22–45, tmb).

tympanal hood One of a pair of tubercles or rounded prominences on the dorsal surface of the first abdominal segment (Lepidoptera).

tympanum (pl., *tympana*) A vibrating membrane; an auditory membrane or eardrum (Figure 2–8D, 22–45, tym).

type genus See **types**.

type species See **types**.

types Specimens designated when a species or group is described to serve as the reference if there is any question about what that species or group includes. The type of a species or subspecies (the holotype) is a specimen, the type of a genus or subgenus is a species, and the type of a tribe, subfamily, family, or superfamily is a genus.

unisexual	Consisting of or involving only females.
uric acid	Chemical commonly used by terrestrial insects for excretion of nitrogenous wastes.
urine	Fluid containing excreted wastes.
urogomphi	(sing., *urogomphus*) Fixed or movable cercuslike processes on the last segment of a beetle larva (also called *pseudocerci* or *corniculi*).
uropod	One of the terminal pair of abdominal appendages, usually lobelike (Crustacea; Figure 5–22, ur).

vagina	The terminal portion of the female reproductive system, which opens to the outside (Figures 2–22, 2–31A, vag).
valvifers	The basal plates of the ovipositor, derived from the basal segment of the gonopods.
valvulae	The three pairs of processes forming the sheath and piercing structures of the ovipositor.
vas deferens	(pl., *vasa deferentia*) The sperm duct leading away from a testis (Figure 2–31B, vd).
vas efferens	(pl., *vasa efferentia*) A short duct connecting a sperm tube in the testis with the vas deferens (Figure 2–31B, ve).
vein	A thickened line in the wing.
venter	The ventral side.
ventrad	Toward the ventral side or underside of the body; downward.
ventral	Lower or underneath; pertaining to the underside of the body.
ventral nerve cord	Paired nerve lying along the lower surface of the hemocoel, containing segmentally arranged ganglia.
ventriculus	Midgut.
vermiform	Wormlike.
vermiform larva	A legless, wormlike larva, without a well-developed head (Figure 2–43A).
vertex	The top of the head, between the eyes and anterior to the occipital suture (Figure 2–13, ver).
vesicle	A sac, bladder, or cyst, often extensible.
vestigial	Small, poorly developed, degenerate, nonfunctional.
vibrissae, oral	See **oral vibrissae**.
vitellarium	Portion of the ovariole in which vitellogenesis takes place.
vitelline membrane	The cell wall of the insect egg; a thin membrane lying beneath the chorion (Figure 2–37, vm).
vitellogenesis	Transfer of vitellogenins to the developing oocyte with consequent increase in size of the oocyte.
vitellogenin	Yolk precursor molecule.
vulva	Opening of the vagina (= ovipore).
vulvar lamina	The posterior margin (usually prolonged posteriorly) of the eighth abdominal sternite (female Anisoptera).

wireworm	An elateriform larva; a larva that is slender, heavily sclerotized, with few hairs on the body, and with thoracic legs but without prolegs; the larva of a click beetle (Figure 26–45B).

Y-vein	Two adjacent veins fusing distally, forming a Y-shaped figure (for example, the anal veins in the front wing, Figure 30–32).

zoophagous	Feeding on animals.

References

Borror, D. J. 1960. Dictionary of Word Roots and Combining Forms. Palo Alto, CA: Mayfield, 134 pp.

Brown, R. W. 1954. Composition of Scientific Words. Washington, DC: Author, 882 pp.

Carpenter, J. R. 1938. An Ecological Glossary. London: Kegan, Paul, Trench, Trubner, 306 pp.

Dorland, W. A. N. 1932. The American Illustrated Medical Dictionary; 16th ed. Philadelphia: W. B. Saunders, 1493 pp.

Gordh, G., and D. H. Headrick. 2001. A Dictionary of Entomology. Wallingford, UK: CABI Pub., 1050 pp.

Hanson, D. R. 1959. A Short Glossary of Entomology with Derivations. Los Angeles: Author, 83 pp.

Henderson, I. F., and W. D. Henderson. 1939. A Dictionary of Scientific Terms. 3rd ed., revised by J. H. Kenneth. London: Oliver and Boyd, 383 pp.

Jaeger, E. C. 1955. A Source Book of Biological Names and Terms. Springfield, IL: C. C. Thomas, 317 pp.

Jardine, N. K. 1913. The Dictionary of Entomology. London: West, Newman, 259 pp.

Nichols, S. W. 1989. The Torre-Bueno Glossary of Entomology. New York: New York Entomological Society, 840 pp.

Pennak, R. W. 1964. Collegiate Dictionary of Zoology. New York: Ronald Press, 583 pp.

Smith, J. B. 1906. Explanation of Terms Used in Entomology. Brooklyn: Brooklyn Entomological Society 154 pp.

Snodgrass, R. E. 1935. Principles of Insect Morphology. New York: McGraw-Hill, 667 pp. (Reprinted in 1993 by Cornell University Press)

Torre-Bueno, J. R. de la. 1937. A Glossary of Entomology. Lancaster, PA: Science Press, 336 pp.

Tuxen, S. L. (Ed.). 1970. Taxonomist's Glossary of Genitalia of Insects, rev. ed. Copenhagen: Munksgaard, 359 pp.

Tweney, C. F., and L. E. C. Hughes (Eds.). 1940. Chambers' Technical Dictionary. New York: Macmillan, 957 pp.

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Froeschner, "Contributions to a synopsis of the Hemiptera of Missouri, pt. I. Scutelleridae, Podopidae, pentatomidae, Cydnidae, Throeocoridae," *American Midland Naturalist* 26(1): 122-146, 1941, fig. 31, 33, 34, 36. Used by permission. 304: Fig. 22-42 from R.C. Froeschner, "Contributions to a synopsis of the Hemiptera of Missouri, pt. I. Scutelleridae, Podopidae, pentatomidae, Cydnidae, Throeocoridae," *American Midland Naturalist* 26(1): 122-146, 1941, fig. 19, 22, 29. Used by permission. 305: Fig. 22-43 used by permission of the Illinois Natural History Survey. 316: Fig. 22-51 from H. Osborn, "The Fulgoridae of Ohio," *Ohio Biological Survey Bulletin* No. 35 6(6):283-357, 1938, fig. 2, 5a, 5b, 5c, 13Aa, 16Bb, 18A, 25, 26A, 27B, 33, 35A, 38B. Used by permission of Ohio Biological Survey, Inc. 317: Fig. 22-53 from G.F. Knowlton and M.J. Janes, "Studies on the biology of Paratrioza cockerelli (Sulc)," *Annals of the Entomological Society of America* Vol. 24, 1931, p. 283-291, pl. 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Chapter 23. 335: Fig. 23-3 from P. Pesson, "Ordre des Thysanopter Haliday, 1836 (Physapoda Burm., 1838) ou thrips" *Traite de Zoologie* 10:1805-1869, 1951, fig. 1647 1619a, fig. 1626B. Used by permission of Masson et Cie, Paris. 336: Fig. 23-4 from L.J. Stannard, "The thrips, or Thysanoptera, of Illinois," *Illinois Natural History Survey Bulletin* 29(4):215-552, figs. 93, 94, 89. Used by permission of the Illinois Natural History Survey. 336: Fig. 23-4a used by permission of the Utah Agricultural Experiment Station. 337: Fig. 23-5 from L.J. Stannard, "The thrips, or Thysanoptera, of Illinois," *Illinois Natural History Survey Bulletin* 29(4):215-552, figs. 62, 64, 65, 66, 68. Used by permission of the Illinois Natural History Survey. 337: Fig. 23-6a from L.A. Mound and R. Marullo, "Two new basal-clade Thysanoptera from California with Old World affinities," *Journal of the New York Entomological Society* 106: 81-94, 1998, Fig. 9. Used by permission. 337: Fig. 23-6b from S.F. Bailey, "The thrips of California, part I: Suborder Terebrantia," Bulletin of the *California Insect Survey* 4(5):143-220, 1957, fig. 20. Used by permission of the Regents of the University of California Press. 337: Fig. 23-6c, d from L.A. Mound, B.S. Heming, and J.M. Palmer, "Phylogenetiv relationships between the families of recent Thysanoptera (Instects)," *Zoological Journal of the Linnean Society* 16: 111-141, 1980, Fig. 39, Fig. 40. Used by permission of Blackwell Publishing.

Chapter 24. 342: Fig. 24-1 from K.M. Sommerman, "Bionomics of Ectopsocus pumilis" *Psyche* 50(3-4): 53-64. Used by permission. 352: Fig. 24-8a, c from K.M. Sommerman, "Description and bionomics of Caecilius manteri n. sp. (Corrodentia)," *Proceedings of the Entomological Society of Washington* 45(2): 29-39, 1943, Pl. I, fig 3 and fig. 4. Used by permission of the Entomological Society of Washington. 352: Fig. 24-8b, e from K.M. Sommerman, "Bionomics of Amapsocus amabilis (Walsh) (Corrodentia, Psocidae)," *Annals of the Entomological Society of America* Vol. 37, 1944, p. 359-364, pl. I fig. 1, fig. 2. Used by permission. 352: Fig. 24-8d from *National Pest Control Association Service Technician's Handbook*, p. 88, Copyright © 1996 by the National Pest Management Association. Used by permission. 352: Fig. 24-8f from A.B. Gurney, "A synopsis of the psocids of the tribe Psyllipsocini, including the description of an unusual new genus from Arizona (Corrodentia: Empheriidae: Empheriinae)," *Annals of the Entomological Society of America* Vol. 36, 1943, p. 195-220. pl. III fig. 23. Used by permission. 352: Fig. 24-8f from A.B. Gurney, "Nomenclatorial notes on Corrodentia, with descriptions of two new species of Archipsocus, *Journal of the Washington Academy of Sciences* 29(11): 501-515, 1939, Fig. 1, p. 503. Used by permission of the Washington Academy of Sciences.

Chapter 25. 357: Fig. 25-1 from R.E. Snodgrass, *Principles of Insect Morphology*, Cornell University Press, 1993, fig. 35C, p. 70.

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Fig. 3 (upper center). Used by permission of the Ohio Academy of Science. 438: Fig. 26-66 from R.H. Arnett, Jr. and M.C. Thomas, *American Beetles*, fig. 1.109, 1.115. The American Entomological Institute, Ann Arbor, MI. Used by permission of CRC Press. 439: Fig. 26-67a, e, f, d from F.G. Werner, W.R. Enns, and F.H. Parker, "The Meloidae of Arizonae," *University of Arizona Agricultural Experiment Station Technical Bulletin* 175, 1966, fig. 59, 64, 96, 103. Used by permission. 439: Fig. 26-67b, c from W.J. Baerg, "Control measures for blister beetles," *Arkansas Agricultural Experiment Station Bulletin* 201, 1925, fig. 1, fig. 2. 439: ig. 26-68 from W.R. Horsfall, "Biology and control of common blister beetles in Arkansas," Arkansas Agricultural Experiment Station Bulletin 436, 1945, Fig. 5, p. 18. Used by permission the Arkansas Agricultural Experiment Station. 440: Fig. 26-69a from R.H. 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Chapter 34. 707: Fig. 34-28 from O.A. Johannsen, "Aquatic Diptera, Part 1, Nemocera, exclusive of Chironomidae and Ceratopogonidae," *Cornell University Agricultural Experiment Station Memoir* 164, 1933, fig. 96. Used by permission. 708: Fig. 34-29 from W.E. Dove, D.G. Hall and J.B Hull, "The salt marsh sand fly problem (Culicoides)," *Annals of the Entomological Society of America* Vol. 25, 1932, p. 505-527, pl. II and pl. III, fig. 2. Used by permission of the Entomological Society of America. 709: Fig. 34-30 from O.A. Johannsen, "Aquatic Diptera, Part 1, Nemocera, exclusive of Chironomidae and Ceratopogonidae," *Cornell University Agricultural Experiment Station Memoir* 164, 1933, fig. 132, fig. 152, fig. 166. Used by permission. 709: Fig. 34-31 from H.E. Branch, "The life history of Chironomus cristatus Fabr. With descriptions of the species" *Journal of the New York Entomological Society* 31:15-30, 1923. 710: Fig. 34-32 from O.A. Johannsen, "Aquatic diptera, Part IV and Part V," *Cornell University Agricultural Experiment Station Memoir* 210, 1937, fig. 134, fig. 135. 710: Fig. 34-33 From O.A. Johannsen, "Aquatic Diptera, Part 1, Nemocera, exclusive of Chironomidae and Ceratopogonidae," *Cornell University Agricultural Experiment Station Memoir* 164, 1933, fig. 173, fig. 187, fig. 188. 711: Fig. 34-35 from T.J. Headlee, *The Mosquitoes of New Jersey and Their Control*, 1945, p 20, 42, 93, 121. Used by permission of Rutgers University Press. 715: Fig. 34-40f, g from O.A. Johannsen, "Aquatic Diptera, Part 1, Nemocera, exclusive of Chironomidae and Ceratopogonidae," *Cornell University Agricultural Experiment Station Memoir* 164, 1933, fig. 209, fig. 210. 718: Fig. 34-45 From B.B. Fulton, "A luminous fly larva with spider traits (Diptera, Mycetophilidae)," *Annals of the Entomological Society of America* Vol. 34, 1941, p. 289-302, pl. II, fig. 4. Used by permission of the Entomological Society of America. 721: Fig. 34-47b from H.H. Ross, "The Rocky Mountain black fly Symphoromyia atripes (Diptera: Rhagionidae)," *Annals of the Entomological Society of America* Vol. 33, 1940, p. 254-257, pl. I, Fig. 1. Used by permission. 722: Fig. 34-49 from H.H. Schwardt and D.G. Hall, "Preliminary studies on Arkansas horse-flies," *Arkansas Agricultural Experiment Station Bulletin* 256, 1930. Used by permission the Arkansas Agricultural Experiment Station. 724: Fug. 34-53 from F.R. Cole, "Notes on Osten Sacken's group; Poecilanthrax, with descriptions of new species," *Journal of the New York Entomological Society* 25:67-80, 1917. 727: Fig. 34-60 from Fig. 3, p. 113 in G.F. Knowlton, "Biological control of the beet leafhopper in Utah," *Proceedings of the Utah Academy of Sciences, Arts, and Letters* 14:111-139, 1937. 728: Fig. 34-61a, b from C.L. Metcalf, "Preliminary report on the life-histories of two species of Syrphidae," *The Ohio Naturalist* 11(7):337-346, 1911. 729: Fig. 34-62 from Alvah Peterson, *Larvae of Insects: An introduction to Nearctic species*, 1948, Vol. II, fig. D31F, D31G, D30D, D32F, D32A. Reprinted by permission. 730: Fig. 34-63 used courtesy of the Ohio Agricultural Research and Development Center. 731: Fig. 34-66 used by permission of the Utah Agricultural Experiment Station. 738: Fig. 34-79 from G.N. Wolcott, "The insects of Puerto Rico," *Journal of Agriculture of the University of Puerto Rico* 32(2): 255-822. Used by permission of the Agricultural Experiment Station of the University of Puerto Rico. 742: Fig. 34-85 from Alvah Peterson, *Larvae of Insects: An introduction to Nearctic species*, 1948, Vol. II, fig. D38A. Reprinted by permission.

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Index

Numbers in italics refer to pages bearing illustrations; numbers in boldface indicate the most important page references. Common names of species and subspecies are listed in the singular; those of more inclusive groups are listed as plurals. Many items not in this index may be found in the glossary.

Alexander Wild (University of California, Davis, USA) -

Borror and Delong's weighty "Introduction to the Study of Insects" enters its 7th edition as the standard text for students of North American insect taxonomy. This latest edition is brought up to date by Charles Triplehorn and Norman Johnson after a 15 year gap.

As in earlier editions, Borror and DeLong is a comprehensive survey of North American insect diversity, containing identification keys for the insects and other arthropods along with brief overviews of each family and tips for collection and specimen preparation. Keys are mostly at the order and family levels of the Linnean hierarchy, with subfamily keys presented for select groups. This text is not a field guide; many groups are not illustrated, or are represented only by line drawings of particular parts of their anatomy. Rather, it is best used as a laboratory reference, a single-volume source for identifying insects and spiders to family. No other single reference has the breadth of this text, so Borror and DeLong should retain its place on the shelf of any serious entomologist.

"Introduction to the Study of Insects" also contains chapters on insect ecology, physiology, and systematics, but these are brief. More appropriate texts for these areas are available elsewhere (for instance, Gullan and Cranston's "An Outline of Entomology".)

The 7th edition has been sorely needed. A recent wealth of DNA sequence data and rapid advances in the methodology and philosophy of systematics have produced a flowering of research on insect relationships. As taxonomic improvements accumulated, the 6th edition- the only resource of its kind- had grown increasingly out of touch with the state of the field. So it should come as no surprise that the most noticeable changes in the new edition (aside from the leafy green cover and smaller font size of the text) are in the classifications. Gone is the order Homoptera, sunk at long last into Hempitera. A number of families have disappeared into synonymy (e.g., Anthophoridae into Apidae), while others have been split out (e.g., Stenopelmatidae from Gryllacrididae). Other changes include a completely new beetle key, a considerably improved treatment of spiders, and the inclusion of a newly-discovered order of African insects, Mantophasmatodea.

Triplehorn and Johnson unfortunately are uneven in adopting taxonomic updates across groups. For instance, the wasp family Sphecidae is retained in spite of a long-standing consensus among Hymenopterists that it does not represent a natural group, while other groups like the calyptrate fly family Fanniidae are split out in spite of a lack of consensus among Dipterists over its status. The authors also mix Linnean ranked categories (Family, Order, etc.) with non-ranked clades in several places, with confusing results. Given the extraordinarily dynamic state of the field, however, the authors can be forgiven for some of their decisions.

Many of the revisions appear hasty, as though the book were primarily product of a publisher's deadline. For example, the utility of Michael Ivie's improved beetle key is marred by its incongruous insertion into the largely unaltered text of the previous edition. The chapter introduction treats the user to explanations of 6th edition characters that no longer appear in the new key, while scores of new and often complex characters are not explained in the text, do not appear in the glossary, and are not illustrated. I had to refer to Arnett's American Beetles numerous times to make sense of the new characters. In fact, with few exceptions (like Trichoptera), the figures have not been updated for several editions and users are left to puzzle over scores of unexplained couplets. Microsetose antennal grooves in Coleoptera? Dorsal versus ventral abdominal spiracles in Lygaeoid bugs? Adequate explanations will not be found in the text.

The editing is sloppy. The formatting of taxonomic synopses appears not to have been checked as there are errors in indentation (e.g., the Calyptrate muscoid fly families are indented equal to their header). Page headers for keys persist well beyond the keys themselves. For instance, scale insect descriptions (pg. 324-328) are found on pages labeled, oddly enough, "Key to the Subfamilies of Cicadellidae." The index is conspicuously error-laden (e.g., the beetle family Ciidae is nowhere to be found, but appears erroneously as "Cidae" and "Cilidae". And who knew that "Cermanbycidae"(sic) were long-horned beetles?). Some figure references in the keys have not caught up to the new arrangement of the illustrations; couplet 53 in the fly key points to an illustration that has since moved elsewhere.

Distressingly, a few errors from the previous edition are left uncorrected, and new errors have been introduced. For example, couplet 11 of the Hymenoptera key still asks users to decide if certain wing crossveins are "present" or "present" (11' should read "absent"). Couplet 14 shunts wingless wasps to couplet 16 (the Apoidea) instead of couplet 106. Most moths in the common family Noctuidae will be incorrectly identified as Pantheidae because of a text error at couplet 59 in the Lepidoptera key.

The family descriptions that follow the keys in each chapter are a mixed bag. Usually they are succinct and accurate, but some of the assessments of North American species numbers are dated. There are occasional taxonomic errors that result from outdated text carried uncritically over from older editions. For example, our Nearctic army ants have been classified in the genus Neivamyrmex since the 1950s, yet the text several editions later still refers to them as Eciton.

ov, oral vibrissae
ovb, outer vertical bristles
ovd, oviduct
ovl, ovariole
ovp, ovipositor
ovt, ovarian tubule
ovy, ovary

p, palp, lateral lobe
P, posterior cell
pa, postabdomen
pab, postalar bristles
pb, posthumeral bristles
pbr, pollen brush
pbs, prebasilare
pc, postalar callus
pcb, precoxal bridge
pclp, postclypeus
pcn, pore canal
pcv, posterior cross vein
pdp, pedipalp
pe, penes
ped, pedicel
pf, pilifer
pg, postgena
pgc, pigment cell
pgl, paraglossa
ph, phragma
phtr, phallotreme
phx, pharynx
pj, poison jaw or toxicognath
pl, pleuron
plap, pleural apophysis
plf, palpifer
plg, palpiger, squama, or proleg
pls, pleural suture, humeral suture
plw, posterolateral wart
pm, postmarginal vein
pmr, paramere
pmt, postmentum
pn, postnodal cross vein
PN, postnotum
pnwp, posterior notal wing process
po, postocciput
pol, postocular lobe of prothorax
por, postoccipital ridge
pos, postoccipital suture
pp, prepectus
ppb, propleural bristles
ppt, paraproct
pr, pollen rake or pecten
prb, proboscis
prc, pronotal comb
prct, proctodeum
prd, propodeum
prl, proleg
prmt, prementum
pro, prosoma
ps, posterior spiracle
psb, presutural bristles
pscl, postscutellum
pscu, pseudocubitus
psl, paired second lobe
psm, pseudomedia
psp, posterior spiracle
pt, pteropleuron
ptar, pretarsus
ptb, pteropleural bristles
ptbr, preapical tibial bristles
ptl, genu or patella
ptp, posterior tentorial pit
ptsp, preapical tibial spur
pul, pulvillus
pv, postvertical bristles
pvp, perivulvar pores
pwp, pleural wing process
py, pygidium

q, quadrangle

r, radial cross vein
R, radial vein
rec, rectum
ret, retina
rg, ring segment
rh, rhabdom
Rs, radial sector
rspl, radial supplement
rv, recurrent vein

s, sectorial cross vein
sa, sensoria
sap, superior appendage
sas, subantennal sulcus
sb, subalare
sbm, subalar muscle
sc, subcostal vein or salivary channel
Sc, subcostal vein, subcostal cell
sca, scapula
scb, scutellar bristles
scl, scutellum
scn, sense cone
scp, scape
scr, scar left on mandible where cusp has broken off
sct, scutum
scv, subcostal vein
sd, subdiscal or subdiscoidal vein
sdp, spiracular disc pore
se, seta
sec, secretion of adult
segn, subesophageal ganglion
sgo, scent gland opening
sgp, subgenital plate
sgr, subgenal ridge
sgs, subgenal sulcus
sh, bivalved shell
sl, suspensory ligament
sld, salivary duct
slg, salivary gland
sm, submarginal vein
SM, submarginal or apical cell
SMD, submedian cell
smf, submedian fold
smm, submedian macroduct
smml, submarginal macroducts
smt, submentum
smv, seminal vesicle
snc, sensory cell
sos, subocular sulcus
sp, spine or spur
spb, supra-alar bristles
spbr, spiracular bristles
spn, spinneret
spr, spiracle
spt, sperm tube
spth, spermatheca
spthg, spermathecal gland
spv, spurious vein
sq, subquadrangle
ss, setal socket
st, stigma
stb, sternopleural bristles
std, stomodaeum or foregut
stg, prosternal groove
stl, mesosternal lobe
stn, sternum
stns, prosternal suture
stp, stipes
stpl, sternopleuron
str, subtriangle
stra, spiracular trachea
strp, stridulatory pegs
sty, style, stylet, or stylus
stys, stylet sac
su, sulcus or suture
sv, stigmal vein
sw, swimmeret

t, tergum
tb, tibia
tbr, tergal bristles
tc, transverse costal vein
tcb, transverse cubital vein
tcl, tarsal claw
te, teeth on prothorax
tg, tegula
th, thorax
thap, thoracic appendages
tl, transverse lanceolate vein
tm, transverse median vein
tmb, tymbal
tmg, tormogen cell
tn, trochantin
tnt, tentorium
tr, trochanter
trb, trichobothria
trd, transverse radial or transverse marginal vein
trg, trichogen cell
tr gills, tracheal gills
tri, triangle
trs, transverse suture
ts, tarsus
tsm, tergosternal muscle
tsp, tibial spur
tst, testis
ttb, tentorial bridge
tub, prosternal tubercle
tv, transverse vesicle
ty, tylus
tym, tympanum

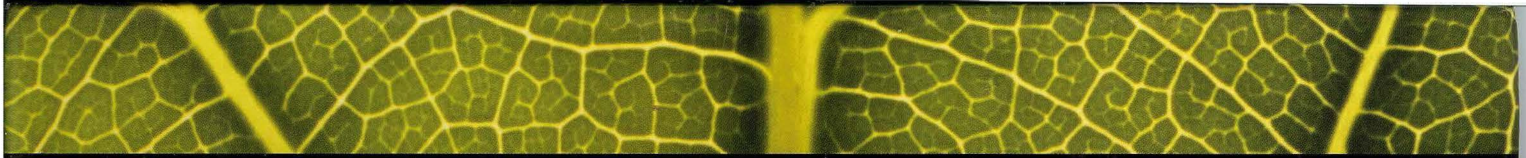
un, uncus
ur, uropod

vag, genital chamber or vagina
vc, ventral circulus
vd, vas deferens
ve, vas efferens
ver, vertex
vlv, ovipositor valvula
vm, vitelline membrane
vnt, ventriculus
vtra, ventral trachea
vu, vulva

w, wing
wb, base of wing

x, connection between axillary sclerite and epipleurite

y, developing young
yc, yolk cell
yo, yolk



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Introduction to the Study of Insects has been the standard text for introductory entomology since it was first published in the 1950s by the late Donald Joyce Borror and Dwight Moore DeLong. In this new Seventh Edition, Triplehorn and Johnson combine the taxonomic approach of this text's definitive study of insects with thoroughly updated coverage of insect biology and evolution as well as insect phylogeny.

Through the text's focus on issues of insect systematics and evolution, you'll learn to appreciate the magnitude of the diversity of insect life as well as the immediate and long-term threats to insect diversity. The thorough insect identification keys and extensive accompanying illustrations make the book an invaluable reference for identification of all of the families of insects found in the continental United States and Canada. Triplehorn and Johnson also provide you with information on up-to-date insect collection methods, such as the use of the Global Positioning System.

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