P

Pachygronthidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Pachyneurid Flies

Members of the family Pachyneuridae (order Diptera).

► Flies

Pachyneuridae

A family of flies (order Diptera). They commonly are known as pachyneurid flies.

► Flies

Pachynomidae

A family of bugs (order Hemiptera).

► Bugs

Pachytroctidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Packard, Alpheus Spring

Alpheus Packard was born on February 19, 1839, at Brunswick, Maine, USA. He graduated from Bowdoin College in 1861, and served from 1864 to 1865 as an assistant surgeon during the American Civil War. After the war he was employed by the Boston Society of Natural History, the Essex Institute, and the Peabody Academy of Science. He was a member of the United States Entomological Commission from 1877 to 1882, and was a professor of zoology and geology at Brown University from 1878 to 1905. Packard (Fig. 1) was a well-rounded naturalist, and wrote on several topics including crustaceans, myriapods, systematic entomology, and economic entomology. He served as chief editor of the journal American Naturalist for 24 years, from 1881 to 1905. He is remembered for his authorship of books including introductory entomology books such as "Guide to the study of insects" (1869), "A text book of entomology" (1898); systematics books such as "Monograph of the geometrid moths or Phalaenidae of the United States" (1876), "Monograph of the bombycine moths of America north of Mexico" in three volumes (1895, 1905, 1914); and economic entomology books such as "Injurious insects, new and little known" (1870), and "Insects injurious to forest and shade trees" (1881). He also authored "Lamarck: the founder of evolution; his life and work, with translations of the writings on organic evolution" in 1901. Packard died at Providence, Rhode Island, on February 14, 1905.

Packard, Alpheus Spring, Figure 1 **Alpheus Packard.**

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Paecilomyces

The genus *Paecilomyces* includes a number of plant, nematode, and insect pathogenic species. Of the fifteen entomopathogenic species, *P. farinosus* and *P. fumosoroseus* are used most often in laboratory studies and are therefore the best described. *Paecilomyces* is characterized by having flask-shaped phialides, or phialides with swollen base structures; the phialides taper into a distinct neck and generate conidia that are dry, hyaline, or slightly pigmented. These conidia adhere end-to-end, forming chains as they emerge. Synnematous growth often occurs on insects.

Paecilomyces farinosus has a broad host range, attacking a number of lepidopterans, coleopterans, hymenopterans and hemipterans. Larval stages of these insects are most readily infected, and a recent report on the identification of fungi infecting gypsy moth larvae shows that *P. farinosus* is actually the most prevalent hyphomycete species in these insects. Eggs of some hosts also can be invaded; for example, *P. farinosus* blastospores were observed to adhere to the sticky surface of sawfly eggs, germinate, and penetrate the egg chorion.

Paecilomyces is cultured easily on agar or under submerged conditions. Media such as Sabouraud dextrose or potato dextrose commonly are used. In one study, it was found that *P. farinosus* conidia produced on Sabouraud dextrose medium containing trehalose accumulated this carbohydrate. Trehalose is known to enhance desiccation tolerance so that propagules with a high content of this sugar may be stored longer, and therefore better suited for biocontrol purposes. It is possible that the trehalose in insect hemolymph provides enhanced survival capabilities to *in vivo*-produced conidia. The pathogenicity of *P. farinosus* towards sawfly larvae is improved by *in vivo* passaging and virulence lost during *in vitro* culture (attenuation) can be restored by passage through living hosts. Additionally, it has been suggested that in vivo growth improves infectivity because this process selects for propagules with relatively high levels of cuticle-degrading enzymes.

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Paederina

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A subtribe of the subfamily Paederinae (Coleoptera: Staphylinidae). It now contains 14 genera, of which the most speciose is *Paederus*. The others are *Paederidus*, *Parameropaederus*, *Lobopaederus*, *Megalopaederus*, *Eupaederus*, *Diplopaederus*, *Oncopaederus*, *Allopaederus*, *Madecapaederus*, *Oreopaederus*, *Pachypaederus*, and *Uncopaederus*. Cladistic methods have not yet been used to study the phylogeny of this subtribe which contains 623 + described species, so the assignment of species to genera is subject to change.

► Dermatitis Linearis
► *Paederus*
► Pederin
► Rove Beetles (Coleoptera: Staphylinidae)

Reference

Frank JH (1988) *Paederus,* sensu lato (Coleoptera: Staphylinidae): an index and review of the taxa. Insecta Mundi 2:97–159

Paederus Fabricius (Coleoptera: Staphylinidae: Paederinae)

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One of the 14 genera of the subtribe Paederina of the subfamily Paederinae of the beetle family Staphylinidae. Hundreds of species of the genus *Paederus* have been described, from all continents except Antarctica and from many islands, especially in the tropics. Nevertheless, they form a very small proportion of the total number of known species of the huge family Staphylinidae (rove beetles).

Adults of most *Paederus* species are unusual among Paederinae in that they are active in broad daylight and climb on vegetation, especially in moist habitats (adults of most other Paederinae, indeed of most Staphylinidae, conceal themselves during daylight hours). Adults of some *Paederus* species are winged and can fly, whereas others are brachypterous or apterous, and flightless. Flight of winged adults has been recorded at night, when they are attracted to incandescent and fluorescent light. Adults of many species are known only from a few specimens, and seem to be rare. Adults of a few are at times very abundant, especially in tropical countries, and some of these serve as useful predators of agricultural pest insects, for example, on rice, maize, and sweetpotato in eastern and southern Asia, South America, and Africa.

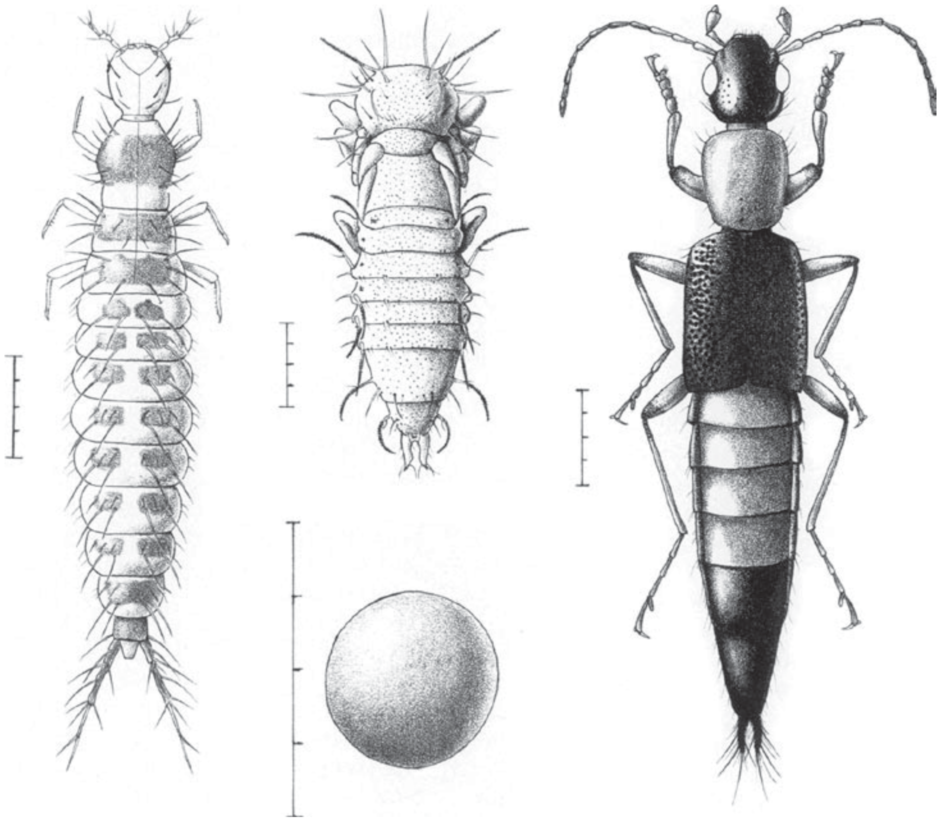
Paederus species (Table 1) have life cycles similar to those of other Staphylinidae, with egg, larval, and pupal stages (Fig. 2). The adult shown has the typical color pattern of black head, orange prothorax, and orange abdomen with black apex, and blue elytra. Like other members of the subfamily Paederinae, the larvae have only two developmental stages (instars); in contrast, most other Staphylinidae have three In temperate regions there may be only one generation per year, but in tropical regions there may be several. Timing and number of generations depends upon climate, in that annual variation (colder temperatures and drier conditions) limit what could become continuous generations under totally favorable conditions. Larvae prey on smaller invertebrates.

That adults of one or more species of *Paederus* produce a chemical toxin was known in Chinese medicine as early as 739 A.D., and the toxin was used medicinally. That adults of some *Paederus* species release toxins when crushed, and these toxins produce dermatitis on human skin was gradually made known to western medicine, beginning in 1901. This gave flying adults of some *Paederus* species pest status in some places and some times of year. The reason is that flying adults are attracted to incandescent and fluorescent light, thus come into contact with humans near such light, may accidentally be crushed by hands or other bodily parts on human skin, and are thus caused to release toxin. The beetles do not attack people! The toxins circulate in the hemolymph of adults, eggs, larvae, and pupae. Those that have caused dermatitis or have experimentally released toxins are listed in the following table.

***Paederus* Fabricius (Coleoptera: Staphylinidae: Paederinae), Table 1 Species causing dermatitis (D) or shown experimentally (E) to produce toxins, with current generic assignment**

Species	Location	D or E
Megalopaederus poweri (Sharp)	Japan	E
Paederidus albipilis (Solsky)	Tadzhikistan	E
Paederidus rubrothoracicus (Goeze)	France, Romania	E
Paederidus ruficollis (F.)	Georgia	E
Paederus alternans Walker	India, Vietnam	D
Paederus amazonicus Sharp	Brazil	D
Paederus brasiliensis Erichson	Argentina, Brazil	D
Paederus brevipennis Lacordaire	Italy	E
Paederus columbinus Laporte	Brazil, Venezuela	D
Paederus cruenticollis Germar	Australia	D
Paederus eximius Reiche = *crebrepunctatus* Eppelsheim	Kenya	D
Paederus ferus Erichson	Argentina	D
Paederus fuscipes Curtis	China, India, Indonesia, Iran, Italy, Japan, Russia, Taiwan, Thailand, Turkey	D
Paederus iliensis Coiffait	Iran	D
Paederus ilsae Bernhauer	Israel, Iran	D
Paederus laetus Erichson	Guatemala	D
Paederus limnophilus Heer	Romania	E
Paederus littoralis Gravenhorst	France, Italy	E
Paederus melampus Erichson	India	D
Paederus melanurus Aragona	Italy	E
Paederus ornaticornis Sharp = *irritans* Chapin	Ecuador	D
Paederus parallelus Weise	Japan	E
Paederus riparius (L.)	Russia	D
Paederus rufocyaneus Bernhauer	Malawi	D
Paederus rutilicornis Erichson	Brazil	E
Paederus sabaeus Erichson	Cameroon, Congo-Brazzaville, Congo-Kinshasa, Namibia, Nigeria, Sierra Leone, Tanzania, Uganda	D
Paederus signaticornis Sharp	Guatemala, Panama	D
Paederus tamulus Erichson	China	D

After Frank and Kanamitsu (1987) with slight update. The 28 species here listed are only a few of the 623 + species of the subtribe, and their generic assignment may change after future taxonomic revisions. Note that one of them is now assigned to genus *Megalopaederus*, and three to genus *Paederidus*. Species causing dermatitis in Malaysia, Papua New Guinea, and Sri Lanka have not been specifically identified.



Paederus Fabricius (Coleoptera: Staphylinidae: Paederinae), Figure 2 ***Paederus*** **egg, larva, and pupa, with** ***P. fuscipes*** **adult. From Frank JH, Kanamitsu K (1987)** ***Paederus*** **sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. J Med Entomol 24:155–191, reproduced by permission of the Entomological Society of America.**

Various early assumptions about the chemical nature, site of production, and purpose of the toxins were later shown to be unfounded. The toxins have not been shown to be present in any group of beetles other than the subtribe Paederina, so are unique among beetles to this subtribe. Further, the toxins have been demonstrated to be present in very few of the species in the subtribe, most of which belong to the genus *Paederus*, whereas their presence could not be demonstrated in some species of the subtribe that have been tested. For the present, we must conclude that the toxins are absent from some, perhaps most, species of the subtribe. The toxins are described under Pederin.

► Dermatitis Linearis
► Paederina
► Pederin
► Rove Beetles (Coleoptera: Staphylinidae)

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Frank JH (1988) *Paederus*, sensu lato (Coleoptera: Staphylinidae): an index and review of the taxa. Insecta Mundi 2:97–159

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Paedogenesis

An unusual form of reproduction in which reproduction commences in the immature stage, usually by activation of the ovaries of immature parthenogenetic females.

Paedomorphosis

The retention of juvenile characters of the ancestral form by the later developmental forms or adult of the modern, descendent form.

Paenibacillus

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Although there are several species of endospore-forming bacteria in the genus *Paenibacillus*, only a few are the causative agents of disease in insects. These are not as well known or studied as the important insecticidal species, *Bacillus thuringiensis*, but they affect economically important insects and therefore have drawn some attention. These bacteria are *Paenibacillus larvae* subsp. *larvae*, *P. larvae* subsp. *pulvifaciens*, *P. popilliae* and *P. lentimorbus*.

Paenibacillus larvae subsp. *larvae* and *P. larvae* subsp. *pulvifaciens* are closely related, having about 90% DNA similarity. However, they are distinguishable at the subspecies level by SDS-PAGE of whole cell proteins, by DNA fingerprinting (AFLP analysis), by a few biochemical tests and by the pathology of the disease produced. *P. larvae* subsp. *larvae* causes American foulbrood and *P. larvae* subsp. *pulvifaciens* causes powdery scale disease in larval honeybees. The bacteria are gram positive, catalase negative and have fastidious nutrition. Larvae are infected by ingesting bacterial spores contaminating their food. Spores germinate in the larval midgut, penetrate the midgut epithelium by phagocytosis and produce a systemic bacteremia resulting in larval death. Vegetative cells sporulate in the dying larvae and provide a source of spores for further infections. Spores can survive for years in larval food, in soil, or in larval cadavers. Adult bees can carry bacterial spores in their digestive tract but are immune to the disease. The bacteria are susceptible to a variety of antibiotics, and oxytetracycline has been used prophylactically or to treat diseased colonies to suppress symptoms. There are reports of the development of bacterial resistance to this antibiotic, and its use is not allowed in some countries.

Paenibacillus popilliae and *P. lentimorbus* are the causative agents of milky disease in various larvae of the family Scarabaeidae. These two species are distinguishable by DNA similarity studies but are quite similar in the usual bacteriological tests. They are facultative, nutritionally fastidious, spore-forming, and present a gram positive cell wall profile although the Gram stain is reported to be negative during vegetative growth. It has been suggested that there should be a single species (*P. popilliae*) and that *P. lentimorbus* should be a subspecies within that species, a situation similar to that of *P. larvae*. The species were originally separated by the production of a parasporal inclusion by *P. popilliae* and the absence of this body in *P. lentimorbus*. However, the DNA similarity study demonstrated that most isolates (although not the type strain) of *P. lentimorbus* also produce paraspores. *P. popilliae*, the subject of most physiological studies, appears to lack a complete tricarboxylic acid cycle and is catalase negative. Although *P. popilliae* grows better in air than without air, growth is better in 10% oxygen than in the 21% oxygen present in air. It is possible that the enzyme deficiencies may be related to the inability of these bacteria to sporulate *in vitro*.

There is no direct evidence that the protein composing the parasporal body plays any role in the course of the disease process. The gene encoding the parasporal protein has been cloned and sequenced, and was shown to have significant similarity to genes encoding the parasporal proteins of *Bacillus thuringiensis*.

The course of infection in scarab larvae is initiated following ingestion of spores. Over the period of 2–4 weeks, spores germinate in the larval gut, vegetative cells penetrate the epithelium, proliferate in the hemolymph, and finally sporulate in the hemolymph. The dead larva displays a turbid or milky hemolymph giving the name "milky disease." As the larval cadaver disintegrates, spores are released into the soil and may be consumed by larvae feeding on plant roots. Insecticides containing *P. popilliae* spores have been produced by collecting larvae in the field, infecting them in the laboratory, blending the spores (and larval debris) with inert carrier, and dispersing the product into soil. Although the bacteria can be grown in bacteriological media, they sporulate poorly outside larvae, and this has frustrated attempts to produce large volumes of spores by fermentation techniques.

The inability of all these insect pathogenic paenibacilli to produce large quantities of spores outside larvae has been the subject of much research. A variety of empirical methods to achieve *in vitro* sporulation have been attempted without success. Until the underlying relationships between sporulation and the peculiarities of the metabolism of these bacteria are better understood, *in vitro* sporulation is likely to remain elusive.

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Paenibacillus larvae = (*Bacillus larvae*) Bacteria

The bacterium responsible for causing American foulbrood in honey bees.

► American Foulbrood
► *Paenibacillus*

Painter, Reginald Henry

Reginald Painter was born on September 12, 1901, at Brownswood, Texas, USA. He received a B.A. (1922) and M.A. (1924) from the University of Texas, and a Ph.D. from Ohio State University (1926). He immediately joined the faculty at Kansas State University, where he remained for his entire career except for brief periods in Honduras and Guatemala. Painter became widely recognized as the leading authority of plant resistance to insects. He worked cooperatively with plant breeders in the production of sorghum, wheat, and alfalfa varieties resistant to insect pests. He also documented the existence of insect biotypes that could overcome host plant resistance. He is remembered for his authorship of "Insect resistance in crop plants," which was the major synthesis and leading work on the subject for decades. Painter also had a strong interest in Bombyliidae, and he and his wife described several new genera and numerous new species from North and Central America, and redescribed many European species. Painter was a fellow of the Entomological Society of America and the American Association for the Advancement of Science, and was awarded the Gamma Sigma Delta International Award for Distinguished Service to Agriculture. He died on December 23, 1968, in Mexico City.

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Anon (1969) Reginald Henry Painter 1901–1969. J Econ Entomol 62:759

Palaeosetidae

A family of moths (order Lepidoptera). They also are known as minature ghost moths.

► Miniature Ghost Moths

► Butterflies and Moths

Palaeosetode

A family of moths (order Lepidoptera). They also are known as minature ghost moths.

► Minature Ghost Moths

► Butterflies and Moths

Palaephatidae

A family of moths (order Lepidoptera). They also are known as Gondwanaland moths.

► Gondwanaland Moths

► Butterflies and Moths

Palearctic Realm

The Palearctic realm is a zoogeographic region encompassing Europe and Asia except for Southeast Asia. The fauna consists of such animals as vireos, wood warblers, deer, bison and wolves, and is quite similar to the fauna of the Nearctic realm (North America). Thus, the Palearctic and Nearctic realms often are combined into a larger region called the Holarctic realm.

► Zoogeographic Realms

Paleoentomology

The study of fossil and extinct insects.

Pale Lice

Members of the family Linognathidae (order Phthiraptera).

► Chewing and Sucking Lice

Paleopterous

Lacking the ability to fold the wings backward over the abdomen.

Pale Western Cutworm, *Agrotis orthogonia* (Morrison) (Lepidoptera: Noctuidae)

The larvae of this moth attack wheat in the Great Plains region of USA.

► Wheat Pests and Their Management

Palidium

A portion of the raster in scarab larvae.

Palindrome

A DNA sequence in two strands that reads the same in both directions.

Pallopteridae

A family of flies (order Diptera). They commonly are known as flutter flies.

► Flies

Palm Beetles

Members of the family Mycteridae (order Coleoptera).

► Beetles

Palmetto Beetles

Members of the family Smicripidae (order Coleoptera).

► Beetles

Palm Insects

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The Palmae are one of the largest plant families, with about 2,600 species. The family is concentrated in the humid lowland tropics, extending to extra-tropical warm regions of the world, including deserts and regions with a Mediterranean climate. A few cold-hardy species can be grown outdoors as far north as Britain. Members of the palm family are easily recognized by their large leaves, or fronds, which occur in two general forms, pinnate and palmate. Palms range in size from less than a meter tall at maturity to arborescent forms such as *Ceroxylon* spp., which may reach a trunk height of more than 65 m and are among the tallest plants in the plant kingdom. Different species have solitary or multiple stems, and stem diameters range from less than a centimeter (e.g., *Chamaedorea* spp.) to 1.8 m in *Jubaea chilensis* (Molina) Baillon.

Palms are important components of the plant communities of warm regions. Their broad fronds and deep leaf axils provide shelter for birds, reptiles, mammals and other animals. The fruits of many species of palms are a prime food source for vertebrate animals. The fronds, leaf axils and stems support a diversity of epiphytes.

Many of the species are sources of economic products, including fruits, beverages, and fiber products. Some species have been cultivated since prehistoric times, notably the coconut palm, *Cocos nucifera* L., the African oil palm, *Elaeis guineensis* Jacquin, the date palm, *Phoenix dactylifera* L., and the peach-palm, *Bactris gasipaes* Kunth. Commercial palm cultivation has expanded along with a general expansion in agriculture beginning in the nineteenth century, and the use of palms as landscape and interior plants has increased dramatically in recent decades. Increasing interest in the culture of palms, along with recognition of the importance of tropical life in the world ecosystem, has stimulated a need for knowledge of the insects associated with these plants.

Palms as Hosts of Insects

The foliage, stems, roots, flowers, and fruits of palms provide food for insects that are undoubtedly important components of their respective ecosystems. Palms constitute a highly stable resource for insects that are adapted to them. They produce foliage periodically throughout the year, so that not only is green tissue continually available to leaf-feeders, but also is present both as fresh foliage and in subsequent stages of maturity. Thus, palms may be food sources for both insects that feed on young foliage and those adapted to feed on mature foliage. The broad fronds are relatively easy targets for insects searching for food sources. Other matters being equal, insects can more readily colonize a large palm leaf than the multitude of small leaves of dicotyledons. The stiff foliage of palms provides superior protection from heavy rain and sunlight. On the other hand, the rigidity of palm foliage is largely due to its high fiber content, which poses a challenge to phytophagous insects.

The stems of palms are highly fibrous, and in some species are extremely hard, especially in the peripheral zone (“rind”). As in monocotyledons in general, the stems, once formed, do not undergo radial growth. There is no cambium or bark, thus no habitat for bark beetles. Some important insect pests of palms are species that bore in the fleshy tissue of buds or rachises. Some insects that bore in the petiole or bud may enter the stem tissue. Few insect species bore directly into palm stems.

The roots of palms are poor nutritionally except at the root tips, and few insects are associated with them.

Palm flowers are generally entomophilous. The inflorescences typically support massive numbers of small, shallow flowers of pale color, often with a strong fragrance. Flowers are produced at different intervals in different species, e.g., monthly in coconut, yearly in date palm, and at the end of the life of the plant in *Corypha* spp.

Although many palm fruits serve as important food resources for vertebrate animals, they are probably less important as food sources for insects.

Severe damage by insects to palms in the wild has been reported, but this is probably rare. As in other crops, palms seem to be most susceptible to destruction by insects when grown in dense monocultures.

The Insect Fauna of Palms

There are striking similarities in the insect fauna associated with palms in different regions. Most of the significant palmivorous insect species are in one of six orders: Orthoptera, Phasmatodea, Hemiptera, Thysanoptera, Coleoptera, and Lepidoptera. Within each of these orders, palmivorous insects are concentrated in particular families, most of which are represented by different species in disparate regions.

Insects that are restricted to palms usually attack a range of several different species of this family, although some insects are restricted to a single genus or species e.g., *Xylastodoris luteolus* Barber (Hemiptera: Thamastocoridae), which is known only on Cuban royal palms, *Roystonea regia* [Kunth] O. F. Cook. Probably no species of insect is adapted to feed on all species of palms. Some palmivorous species also feed on bananas, pandans, or other large monocotyledons, but not on dicotyledons. Many of the pests of palms in cultivation are highly polyphagous species that also attack dicotyledons, such as citrus, coffee, cacao, etc.

The diversity of palmivorous insects in different regions tends to reflect the respective diversity of palms: greater numbers of palmivorous species are known in regions rich in palms, including Southeast Asia and South America, and fewer in regions poor in palm diversity such as tropical Africa.

Defoliators

Caterpillars (Lepidoptera) that feed on palm foliage are found in virtually all palm-growing regions except desert regions, such as in North Africa and the Middle East. Psychidae, Gelechioidea, Zygaenidae, Limacodidae, Hesperiidae, and Nymphalidae are represented by species on palms in most regions.

Important species of bagworms (Psychidae) on palms include *Oiketicus kirbyi* Guilding in tropical America, and *Metissa plana* Walker, *Cremastopsyche pendula* Joanna, and *Mahasena corbetti* Tams (the coconut case caterpillar), in Southeast Asia.

Species of Gelechioidea include the coconut blackheaded caterpillar, *Opisina arenosella* Walker (Oecophoridae), of southern Asia, the coconut flat moth, *Agonoxena argaula* Meyrick (Agonoxenidae) of Oceania, and the palm leaf skeletonizer, *Homaledra sabalella* (Chambers)(Coleophoridae) of the southeastern U.S. and western Caribbean.

The coconut leaf moth, *Artona catoxantha* Hampson, of Southeast Asia, and *Homophylotis catori* Jordan, a pest of coconut palms in West Africa, are two of several important species of palmivorous Zygaenidae. The levuana moth, *Levuana iridescens* Bethune-Baker, decimated coconut plantations in Fiji in the early part of the twentieth century, but became nearly (or possibly completely) extinct as a result of a famous biological control campaign in which *Bessa remota* Aldrich (Diptera: Tachinidae), a natural enemy of *A. catoxantha* in the Malay Peninsula, was imported and established in Fiji.

Species of the zygaenoid family Limacodidae occur on palms in probably all humid tropical regions, and are richest in Southeast Asia, where more than 60 species have been reported on palms. Certain species of Limacodidae are among the most damaging of palm defoliators.

Larvae of many species of skippers (Hesperiidae) feed on monocotyledons, and species of this family are defoliators on palms in most humid tropical regions.

The brushfooted butterflies (Nymphalidae) are represented on palms in the eastern hemisphere by species of Amathusiinae, and in the western hemisphere by Brassolinae and Satyrinae. The adults are large, showy butterflies, much sought after by collectors, and their large, gregarious larvae are highly destructive to foliage.

Worldwide, beetles (Coleoptera) are second in importance to Lepidoptera as palm defoliators, but in certain localities they may equal or surpass Lepidoptera in this respect. Most are in the subfamily Hispinae of the leaf beetle family Chrysomelidae. Most are leaf miners, but a few are superficial leaf feeders.

Several species each of walking-sticks (Phasmatodea) and longhorned grasshoppers (Orthoptera: Tettigoniidae) are important pests of coconut palms in some islands of Oceania. They are polyphagous, their status as pests of coconut palms reflecting the overwhelming importance of these palms on some Pacific islands.

Sap-Feeders

Relatively few true bugs (Hemiptera: Heteroptera) feed on palm foliage, but several species are important pests. *Stephanitis typica* Distant (Tingidae) is widely distributed on coconut palms, bananas, and probably other arborescent monocotyledons in Asia. It is sometimes considered a pest in coconut palm nurseries, and has been shown to be a vector of Kerala coconut decline, also known as coconut root (wilt) disease, of mature coconut palm in southern Asia.

Thaumastocoridae are a small family closely related to Tingidae with 17 known species, six of which are found in the western hemisphere, specifically on palms in tropical America. The 11 eastern hemisphere species are associated with various dicotyledons.

There are only two species of Miridae, the largest family of Heteroptera, of significance on palms: *Carvalhoia arecae* Miller and China, a pest of betel-nut palm, *Areca catechu* L., in India, and *Parasthenaridea arecae* Miller, which has a similar biology in the Malay Peninsula.

Several species of *Lincus* (Pentatomidae) are considered vectors of protozoans that cause marchitez sorpresiva (sudden wilt) of African oil palm, and heartrot of coconut palms, respectively, in northern South America.

The Auchenorrhyncha on palm foliage are much more diverse than the Heteroptera. As in other major taxa, palmivorous species are concentrated in certain families, notably the superfamily Fulgoroidea (planthoppers). The fulgoroid family Derbidae has the highest diversity and widest distribution of Auchenorrhyncha on palms. Only the adults visit palms, typically in sparse numbers. Their nymphs are believed to feed on fungi, and the numbers on palms of one species, *Cedusa inflata* (Ball), were shown to be related to the proximity of decaying plant debris.

Although Cixiidae are less diverse on palms than Derbidae, a few palm-associated species of this family are widely distributed. Attention has been drawn to this family because two species are considered vectors of palm diseases. *Myndus crudus* Van Duzee is a vector of lethal yellowing (LY), which affects almost 40 species of palms in Florida and parts of the Caribbean Region. This insect passes its immature stages on grasses and the adults move to palms. Thus, ground cover management in plantations has been investigated as a method of reducing LY vector populations. *Myndus taffini* Bonfils is a vector of foliar decay of coconut palm in Vanuatu.

Although Cicadellidae are the largest family of Auchenorrhyncha, leafhoppers are not well represented on palm foliage.

The Sternorrhyncha are the best represented suborder on palms, Coccoidea accounting for most of this diversity. Of the few aphid species (Aphididae) reported on palms, two very similar species of *Cerataphis* of an unusual aphid subfamily, Hormaphidinae, have been spread to many tropical countries where they are known only on palms and considered occasional pests. Often their presence is signaled by a thick crust of sootymold over the palm foliage, along with multitudes of honeydew-seeking ants. In their native Southeast Asia, they alternate between palms and certain dicotyledonous trees.

Whiteflies (Aleyrodidae) are more diverse in the tropics than the Aphididae, and nearly 50 species have been reported on palms. Whiteflies probably can be found on palms in most tropical localities, but are not known on date palms in arid regions. Their populations are typically sparse, except in a few recorded cases in which whiteflies recently introduced into new areas have achieved dense enough populations to be considered pests.

Ten of the 20 families of the superfamily Coccoidea have species reported on palms, and it is the superfamily of insects represented on palms by the most species. Palms appear to be particularly favorable hosts for these insects. Coccoidea invade new host plants primarily via the wingless crawler stage (first instar), thus the large fronds of palms and their "evergreen" quality (i.e., continual availability) facilitate the establishment of these passively dispersed insects, and their fibrous tissues provide firm surfaces upon which Coccoidea fabricate their scales. The larger coccoid families, viz., mealybugs (Pseudococcidae), soft scale insects (Coccidae), and armored scale insects (Diaspididae), each contain numerous species that infest palms, and species of each group are known only on palms. As discussed below, several taxa of Coccoidea have special relationships with palms.

The armored scale insects comprise the largest family of Coccoidea. Of the more than 100 species of this family reported from palms, about 15 are recognized as important pests of these plants. Most of the latter are widely distributed, polyphagous insects that are pests of various crop trees and ornamental plants in addition to palms. Among the most notorious of these is the coconut scale, *Aspidiotus destructor* (Signoret), which originated in the tropics of the eastern hemisphere and is now pantropical. Classical biological control of this insect has been successful in many countries but not in others.

The white date scale, *Parlatoria blanchardi* (Targioni-Tozzetti), is an example of an armored scale insect reported exclusively on palms. It is especially frequent on palms of the date palm genus, *Phoenix*. Native to North Africa and the Middle East, where it is sometimes a serious pest, it was introduced accidentally into the date-growing region of the southwestern U.S. during the late 1800s, but was eradicated after a long campaign.

Several families of Coccoidea have special relationships with palms and are thus of exceptional interest to coccidologists. The pit-scale family, Asterolecaniidae, has about 400 species, 29 of which are reported only from palms. Many species of this family induce pit-like galls on their hosts, a characteristic not shared with the palm-infesting species. Phoenicococcidae and Halimococcidae are restricted to palms and related monocotyledons, as is *Comstockiella*, which is a genus of uncertain familial status. Beesoniidae are a family of nine species, four of which are found on palms in tropical America. Curiously, the five species native to the tropics of the eastern hemisphere are gall-makers on dicotyledonous trees.

Thysanoptera are usually not particularly common on palms, but certain species, including the greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouché), a ubiquitous and highly polyphagous pest, sometimes causes superficial damage to palm foliage.

Pests of Flowers and Fruits

The inflorescences of palms may be attacked by various insects, whose feeding causes immature dropping of flowers and fruits. Examples include caterpillars of *Tirathaba* spp. (Galleriidae) and *Batachedra* spp. (Coleophoridae), and a stink bug, *Axiagastus cambelli* Distant (Hemiptera: Pentatomidae). Some species of weevils consume floral parts of palms, in the process serving as pollinators.

Fruits of palms are more important food sources for birds and mammals than for insects. Certain true bugs (Hemiptera: Heteroptera) including *Amblypelta cocophaga* China in the Solomon Islands and *Pseudotheraptus wayi* Brown (Coreidae) in Africa, attack fruits of various plants including young coconut fruits, causing premature fruit-drop. Scale insects that infest palm fruits are generally eurymerous species that also infest leaves, stems, etc.

Nitidulid beetles such as *Carpophilus hemipterus* (L.), *C. dimidiatus* (F.), *C. humeralis* (F.), and *Haptoncus luteolus* (Erichson), are economically important pests of ripening and curing dates in the Coachella Valley of California. Certain varieties of dates are very susceptible to the date stone beetle, *Coccotrypes dactyliperda* (F.) (Scolytinae). Females of this beetle oviposit in unripened fruit and the larvae penetrate the seed and develop inside, while subsequent generations may develop in fruit tissue.

Fruit flies (Diptera: Tephritidae), a major fruit infesting family, do not normally infest palm fruits.

Bud, Petiole, Stem and Root Borers

Several species of scarab beetles (Scarabaeidae) in the subfamily Dynastinae are pests of palms, the most notorious of which is the coconut rhinoceros beetle, *Oryctes rhinoceros* L., a pest of coconut palm in Oceania. The adults bore into the bud, so that when the leaves unfold, large portions have been consumed. The grubs live in decaying vegetation. Several additional species of *Oryctes* are pests of palms in Asia and Africa. In tropical America, several species of *Strategus* are known to bore in the stem bases, or in roots of seedling palms.

Jebusea hammerschmidti Reich (Coleoptera: Cerambycidae) is an important pest of date palms. The adult longhorned beetle females oviposit on palm foliage, and larvae bore into petioles and eventually may enter the trunk.

Dinapate wrightii Horn (Coleoptera: Bostrichidae) bores into the crown and then down into trunk of mature palms, including *Washingtonia* spp. and *Phoenix* spp. Known until recently only in southern California, this species has extended its range in the southwestern U.S. This largest bostrichid in the world (30–50 mm long) makes extensive galleries that weaken the trunk so that it may break in high winds. *Dinapate hughleechi* Cooper is a similar species on palms in Mexico.

The grubs of several species of *Rhynchophorus* (Coleoptera: Curculionidae) bore in the meristem (bud) and sometimes from there into the stems of palms. These weevils include *R. palmarum* (L.) in the American tropics, *R. cruentatus* (F.) in the southeastern U.S., *R. phoenicis* (F.) in Africa, and *R. ferrigeneus* Olivier, the latter which is currently the most widely distributed, having been spread from Asia and Oceania to Africa, the Middle East, and more recently to Southern Europe. *Rhynchophorus palmarum* is a significant pest by itself but it can also vector the red ring nematode, *Bursaphelenchus cocophilus* (Cobb), which causes red ring, a lethal disease of coconut and African oil palms in the American tropics, and little leaf, a chronic disease of these palms.

A second group of weevils important on palms is the tribe Sphenophorini, the New and Old World billbugs. *Metamasius* has 15 species that are reported on palms in tropical America. *Metamasius hemipterus* (L.), considered probably the most damaging, bores into petiole bases, often causing enough damage that they break off. Sometimes they penetrate far enough into the stem to cause superficial damage. *Rhabdoscelus obscurus* (Boisduval) causes similar damage to palms in Queensland, Australia.

Ambrosia beetles (Curculionidae: Scolytinae and Platypodinae) are among the few beetles that bore directly into palm stems (not via the bud or petioles). Extremely small insects, they make narrow galleries in which they culture specific fungi on which they feed. They do not feed on the tissue of palms themselves. They usually attack only stressed palms.

Castnia daedalus Cramer (Lepidoptera: Castniidae) is a large moth whose caterpillars bore between petiole bases and the trunk of palms, causing the fronds to buckle and sometimes damaging the stem surface. It is widely distributed in South America.

Opogona sacchari (Bojer)(Lepidoptera: Tineidae) is a small moth whose larvae bore in stems of various monocotyledons, including some palms, mostly under nursery conditions. The larvae are apt to begin the attack by feeding on damaged stem tissue, and then may continue feeding and making a gallery in healthy stem tissue, at times penetrating into the roots.

The larvae of *Sagalassa valida* Walker (Lepidoptera: Glyphipterigidae) bore in roots of African oil palm in Colombia. Females oviposit near the base of the stems, from which the larvae penetrate the roots, hollowing them out and sometimes causing extensive death of primary roots.

Pollinators

Although in date palms and other species, pollen transfer is partially or exclusively anemophilous, i.e., by air currents, the vast majority of palm species have entomophilous flowers, i.e., that are pollinated by insects. Thus, palm flowers are often scenes of intense insect life. Coleoptera, Hymenoptera, and Diptera are the best-represented orders. Weevils (Coleoptera: Curculionidae) and stingless bees (Hymenoptera: Apidae: Meliponinae) are particularly important. Lepidoptera are of far less importance in palm pollination. Other insects, e.g., Thysanoptera, may be significant in pollinating some species in some localities. Some pollinators, e.g., certain weevils, also consume somatic floral tissue, the damage of which may be vastly offset by their benefits as pollinators. *Elaeidobius kamerunicus* (Faust) (Curculionidae), the major pollinator of African oil palm in West Africa, has been introduced into other tropical countries to increase fruit production in this palm.

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Palm Moths (Lepidoptera: Agonoxenidae)

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Palm moths, family Agonoxenidae, are a small family of 68 known species, in all faunal regions for subfamily Blastodacninae but only South Pacific for four of the species of subfamily Agonoxeninae (plus one from Argentina). The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (6–15 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi recurved; maxillary palpi small, 1-segmented. Wings elongated, usually with very narrow hindwings with long fringes. Maculation varied, often yellow or brown shades with some markings, but a few are colorful and with iridescent markings. Adults are diurnal. Larvae are leaf skeletonizers, or borers in leaves, stems, and fruits; rarely gall-makers. Host plants mostly in Rosaceae for Blastodacninae and Palmae for Agonoxeninae. A few are economic.

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Palm Scales

Members of the families Phoenicococcidae and Halimococcidae, superfamily Coccoidea (order Hemiptera).

► Scale Insects and Mealybugs

► Bugs

Palm, Thure

Thure Palm was born near Ystad in southern Sweden on January 30, 1894. He became interested in insects as a child, and in 1918 became a forestry officer. About 1926 he began to study beetles of importance to forestry and in 1951 published a book on insects of importance to wood and bark in northern Sweden, and in 1959 another for middle and southern Sweden. He also published over 200 papers on systematics, ecology, and faunistics, and was one of the most recognized Swedish coleopterists of modern time. He received an honorary doctoral degree from the University of Lund in 1953. He died at Malmö, Sweden, on May 2, 1987.

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Palp (pl., palps)

Small, paired, segmented sensory appendages attached to the maxilla or labium; more correctly called palpus (Figs. 3 and 4).

► Palpus

► Mouthparts of Hexapods

Palpifer

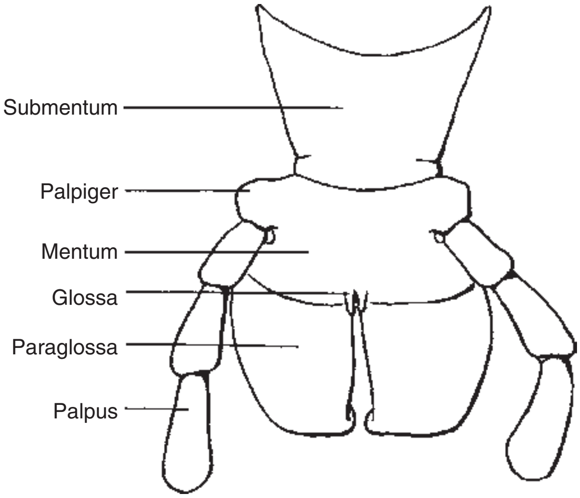
A small sclerite that bears the maxillary palpus, and is connected to the stipes.

► Mouthparts of Hexapods

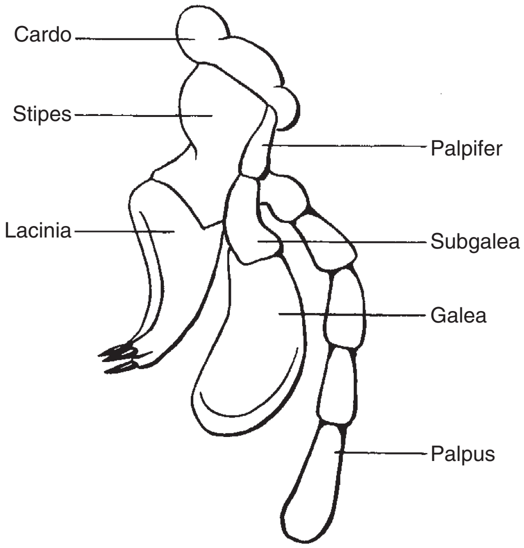
Palpiger

A small sclerite that bears the labial palpus, and is connected to the mentum (Fig. 4).

► Mouthparts of Hexapods



Palp (pl., palps), Figure 3 External aspect of the labium in an adult grasshopper, showing some major elements.



Palpiger, Figure 4 **External lateral aspect of the left maxilla in an adult grasshopper, showing some major elements.**

Palpus (pl., palpi)

Small, paired, segmented sensory appendages attached to the maxilla or labium; also called palp (Figs. 3 and 4).

► Mouthparts of Hexapods

Pamphilidae

A family of sawflies (order Hymenoptera, Suborder Symphyta). They commonly are known as web-spinning or leaf-rolling sawflies.

► Wasps, Ants, Bees and Sawflies

Pamphiliidae

A family of sawflies (order Hymenoptera, suborder Symphyta). They commonly are known as web-spinning or leaf-rolling sawflies.

► Wasps, Ants, Bees and Sawflies

Panoistic Ovaries

Ovaries in which the oocytes lack nurse cells (contrast with meroistic ovaries).

Panorpidae

A family of scorpionflies (order Mecoptera). They are known as common scorpionflies.

► Scorpionflies

Panorpodidae

A family of scorpionflies (order Mecoptera). They commonly are known as short-faced scorpionflies.

► Scorpionflies

Panthophthalmidae

A family of flies (order Diptera).

► Flies

Panzootic

A condition wherein a disease affects all, or a large proportion of the animals of a region; extensively epizootic.

Paper Wasps

Members of the family Vespidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Papilionidae

A family of butterflies (order Lepidoptera). They commonly are known as swallowtails.

► Swallowtails

► Butterflies and Moths

Papilla (pl., papillae)

A small nipple-like elevation.

Parabiosis

Use of the same nest and sometimes the same odor trails by colonies of different species, which nevertheless maintain separate broods.

Paradichlorobenzene

This solid, white, aromatic product is also known as 1,4 dichlorobenzene. It is most commonly used as a deodorizer in urinals, but also as an insect repellent and insecticide to protect wool products from clothes moths and dermestid beetles. It is sold as "moth flakes" and "para crystals," among others, and competes with naphthalene for this market. It sublimates are room temperatures, forming a vapor, and has proven useful to entomologists to protect insect collections from dermestids. Its toxicity should be considered, however, if prolonged exposure is anticipated. Outdoor uses include application around the bases of fruit trees to deter oviposition and survival of wood boring insects such as peach tree borer, *Synanthedon exitiosa* (Lepidoptera: Sesiidae), though this is not a legal use in all areas.

Paraglossa

A paired labial structure, often jointed, found at each side of the ligula.

► Mouthparts of Hexapods

Parajapygidae

A family of diplurans (order Diplura).

► Diplurans

Parallel Evolution

The evolution along similar lines by taxa that were separated geographically at an earlier stage in history.

Parameres

Structures in the male genitalia of insects; lobes at the base of the aedeagus.

► Abdomen of Hexapods

Paraphrynoveliidae

A family of bugs (order Hemiptera).

► Bugs

Paraphyletic

A taxonomic group that does not include all the descendents of an ancestral form.

► Phylogenetics

Paraphyletic Group

Taxa that do not contain all the recent descendents of a single past species. Insect orders are now not clearly polyphyletic, though some artificial classifications in the past or present are polyphyletic (e.g., grouping all wingless insects into a single taxon) (contrast with polyphyletic and monophyletic groups).

Parapodium

Primitive or false legs or feet. Segmented abdominal processes of symphylans.

Paraproct

One of the two lobes bordering the anus and formed from the ventrolateral parts of the epiproct.

► Abdomen of Hexapods

Parasite

An organism that obtains its food by feeding on the body of another organism, its host, without killing the host.

Parasitic Castration

Any process that interferes with or inhibits the production of mature ova or spermatozoa in the gonads of an organism.

Parasitic Flat Bark Beetles

Members of the family Passandridae (order Coleoptera).

► Beetles

Parasitic Hymenoptera (Parasitica)

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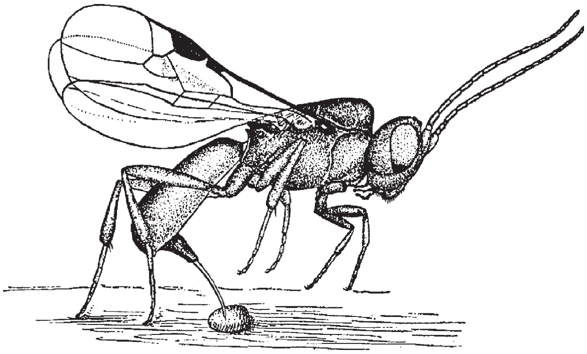
The order Hymenoptera has traditionally been separated into three groups: the suborder Symphyta (sawflies), and the suborder Apocrita, which is subdivided into the Aculeata (bees, wasps and ants) and Parasitica (= Terebrantia). Whereas the Symphyta are monophyletic and the Aculeata holophyletic, the Parasitica are a paraphyletic assemblage of taxa that does not have a formal taxonomic status. But the families comprising the Parasitica share a similarity in basal biology and fill important ecological niches that are of great economic importance, which makes the group a useful one to distinguish. When discussing this group, most modern workers use the term "parasitoid" to denote insects whose larvae feed on and usually kill an arthropod host, to distinguish them from true parasites, which generally do not kill their hosts. The higher classification is still unsettled, but one current scheme recognizes 11 superfamilies and 48 families. Other hymenopteran parasitoids are found in both the Symphyta (family Orussidae) and Aculeata (superfamily Chysidoidea and families Scoliidae, Tiphiidae, Mutillidae, Sapygidae, Pompilidae, Rhopalosomatidae and Bradynobaenidae) (Fig. 5).

Adult Morphology

Given their paraphyletic status, the Parasitica have no unique morphological character, though they are usually smaller and have reduced wing venation compared to the symphyta and Aculeata. Additionally, the Symphyta have no constriction between their first (propodeum) and second (petiole) abdominal segment (although in some very small Parasitica the petiole is reduced in size, and the constriction is not easily evident), while the ovipositor in the Aculeata has been modified to form a sting and no longer acts as an egg-placing device. Adult Parasitica range in body length (excluding antennae and ovipositors) from 0.2 mm to 6 cm, but the vast majority are 5 mm or less. The reduction or absence of wings is found in many families.



Parasitic Hymenoptera (Parasitica), Figure 5 **Adult of *Chelonous shoshoneanorum* Viereck (Hymenoptera: Braconidae) ovipositing within egg of moth (from U.S. Department of Agriculture).**

Parasitic Hymenoptera (Parasitica), Table 2 **Families of the parasitica, their mode of parasitism, and hosts**

				Mode		Host	
Superfamily	**Family**	**1°**	**2°**	**Hemi**	**Holo**	**Arach**	**Phyto**
Ichneumonoidea	Braconidae	++	+	++	++		+
	Ichneumonidae	++	++	++	++	++	
Evanioidea	Evaniidae	++		++			
	Gasteruptiidae	++			++		
	Aulacidae	++			++		
Stephanoidea	Stephanidae	++			++		
Megalyroidea	Megalyridae	++			++		
Trigonalyoidea	Trigonalyidae	++	++		++		
Cynipoidea	Ibaliidae	++			++		
	Liopteridae	++			++		
	Figitidae	++	++		++		
	Cynipidae	N/A	N/A			++	
Proctotrupoidea	Vanhorniidae	++			++		
	Pelecinidae	++			++		
	Austroniidae						
	Maamingidae						
	Monomachidae	++			++		
	Peradeniidae						
	Renyxidae						
	Roproniidae				?		
	Heloridae	++			++		
	Diapriidae	++	+		++		
	Proctotrupidae	++			++		
Platygastroidea	Scelionidae	++	+	++	++	++	
Platygastridae		++		++	++		++
Ceraphronoidea	Ceraphronidae	++	++	++	++		
	Megaspilidae	++	++	++	++		
Mymarommatoidea	Mymarommatidae						

Parasitic Hymenoptera (Parasitica), Table 2 **Families of the parasitica, their mode of parasitism, and hosts (Continued)**

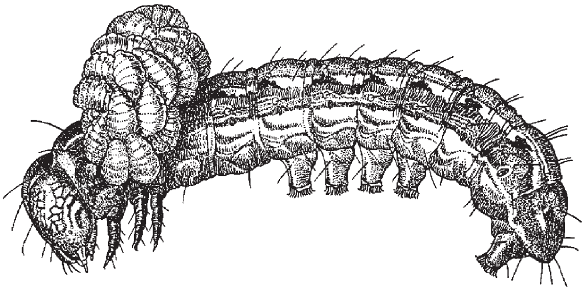
				Mode		Host	
Superfamily	**Family**	**1°**	**2°**	**Hemi**	**Holo**	**Arach**	**Phyto**
Chalcidoidea	Mymaridae	++		++	++		
	Chalcididae	++	++		++		
	Leucospidae	++			++		
	Eurytomidae	++	+	++	++	+	++
	Pteromalidae	++	++	++	++	+	+
	Agaonidae	N/A	N/A			++	
	Torymidae	++	+	++	++		+
	Ormyridae	++	+?		++		
	Perilampidae	++	++	++	++		
	Eucharitidae	++			++		
	Eupelmidae	++	++	++	++	++	
	Tanaostigmatidae	++			++		++
	Encyrtidae	++	++	++	++	++	
	Aphelinidae	++	++	++	++		
	Signiphoridae	++	++	++	++		
	Tetracampidae	++			++		
	Rotoitidae						
	Eulophidae	++	++	++	++	++	+
	Elasmidae	++	++		++		
	Trichogrammatidae	++	+	++	++		

Sexual dimorphism occurs in several groups as well, but is usually limited to differences in antennae, abdominal morphology and color patterns; the most extreme cases are found in the Agaonidae, which have been highly modified as pollinators of figs.

Immature Stages

There are several morphological egg types. The hymenopteriform is several times longer than wide with rounded poles, and is the most common. The acuminate egg is typically long and narrow, and is adapted for extrusion from longer ovipositors. The stalked egg is elongate with a constricted stalk-like projection from one or both poles. The pedicellate egg is a modification of the stalked egg, in which one end is anchored to the host. The encyrtidiform egg resembles a double-bodied dumbbell while in the ovary, but after oviposition one end collapses and it then resembles a stalked egg. Eggs also can be (Fig. 6) classified as lecithal (which are relatively larger and more yolky), or alecithal (which are smaller and physiologically less expensive to produce).

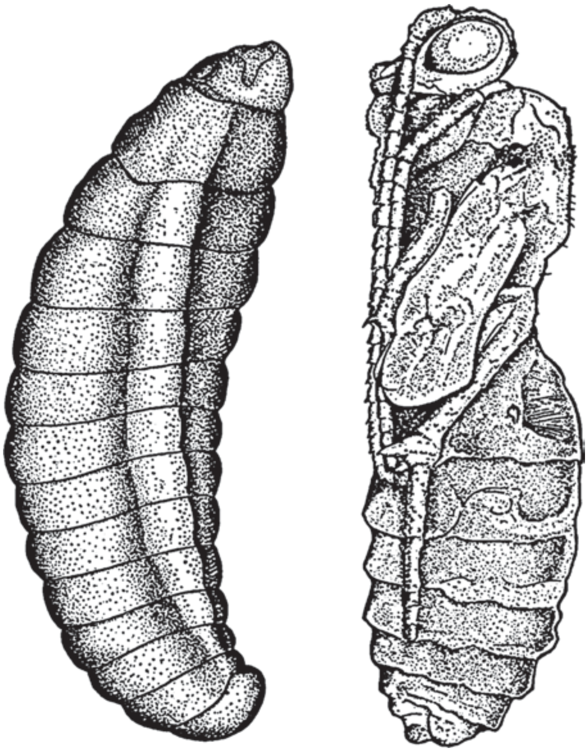
There are one to five larval instars. The greatest variation in morphology occurs in the first instar, where up to 14 types have been distinguished. The most common is hymenopteriform, which is spindle-shaped and maggotlike, and is generally smooth without any conspicuous structures. Subsequent



Parasitic Hymenoptera (Parasitica), Figure 6 **Larvae of an ectoparasitic wasp, *Euplectrus* sp. (Hymenoptera: Eulophidae) feeding externally on a caterpillar (from USDA).**

instars of almost all families take this form as well, and their identification can be very difficult, though families may be distinguished by their scleriterized head structures. Another larval form is the planidium of Eucharitidae and Perilampidae, which is a free-living stage that actively seeks out its host, and has heavier body scleritization. Adult solitary parasitoids optimally deposit only one egg per host. Under some conditions, when more than one egg is deposited, superparasitism may occur, leading to competition between the hatching larvae. Some larvae have well-developed mandibles which can destroy competitors physically, while physiological suppression, selective starvation and suffocation may suppress the supernumerary larvae, although the exact mechanisms are not yet fully understood. In some polyembryonic broods, a precocious "guard" morph is produced that defends its siblings from other larvae, but fails to mature itself. Larvae have a closed midgut, so they cannot expel waste which may foul their environment. Upon completion of feeding, the larvae enter a prepupal stage, when the midgut opens, and the stored wastes are finally expelled and bundled with the last larval skin as a meconial pellet (Fig. 7).

The larvae of many species pupate within the host remains, and do not spin cocoons. Upon death, some hosts become mummified, which effectively provides the same protection to the parasitoid pupa as a cocoon does, but without the physiological expenditure of producing silk. However, most of the Ichneumonidea and a few Chalcidoidea do produce silk cocoons, some of the most notable being gregarious microgastrine braconids, which feed internally in their Lepidoptera hosts, but emerge to pupate on the outside of their host by the dozens.



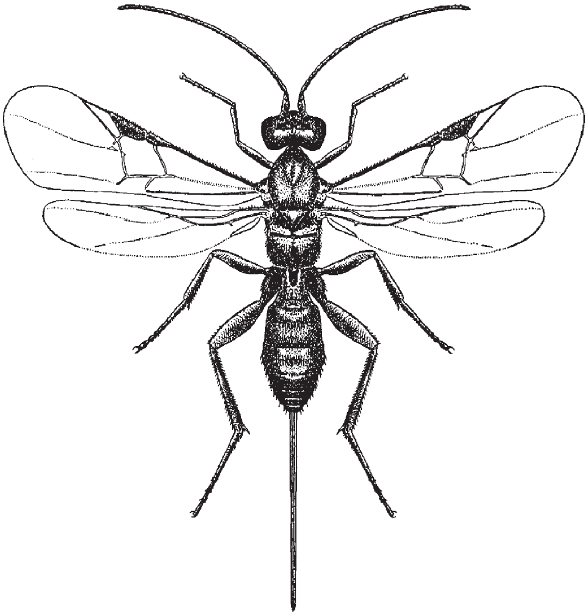
Parasitic Hymenoptera (Parasitica), Figure 7 **The larval (*left*) and pupal (*right*) stages of an endoparasitic wasp, *Agathis gibbosas* (Say) (Hymenoptera: Braconidae) (from USDA).**

Biology

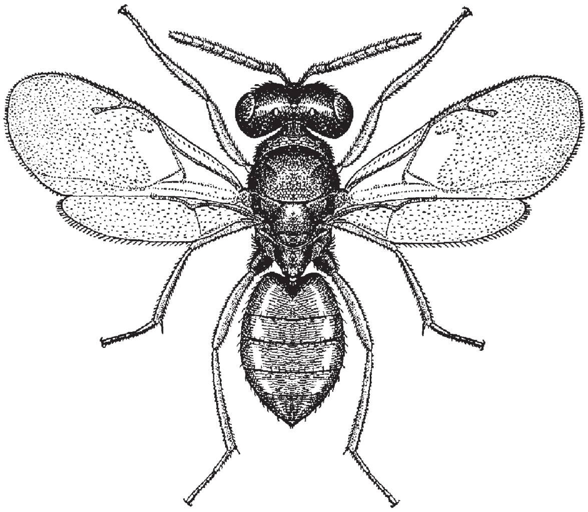
Like other Hymenoptera, most of the Parasitica have a haplo-diploid reproductive strategy, where a fertilized (diploid) egg produces a female, and an unfertilized (haploid) egg produces a male (arrhenotokous parthenogenesis). Thus, by controlling fertilization, ovipositing females can choose what sex egg to allocate after inspecting the prospective host. In some groups, thelytokous parthenogenesis occurs, where males are unknown and unfertilized females produce only females. In several groups of Chalcidoidea, thelytoky can be induced through infection by *Wolbachia* bacteria. Finally, deuterotokous parthenogenesis occurs in a few species, where unfertilized eggs can produce both males and females; in this case, males appear to be sexually non-functional. Two strategies of egg-production have been characterized in the Parasitica: synovigenesis, where females successively develop a number of eggs (generally lecithal), throughout her lifetime, and proovigenesis, where ovigenesis is completed soon after females emerge from the pupa, and thus have only a fixed number of eggs (generally alecithal) to lay (Fig. 8).

In some groups, adult morphology varies based on environmental factors, typically depending upon the size or choice of host. The most dramatic changes occur in the gall-inducing Cynipidae, which undergo an alternation of generations (heterogony) – a sexual generation of females and males, and a non-sexual (agamic) generation of females. Often the adult morphology and the gall structure and site differs considerably between the two generations.

Parasitoids can be classified in several ways. (i) Endoparasitoids develop internally in the host, and ectoparasitoids develop externally (though a few species may begin their development internally and finish externally). (ii) They also can be separated based on the variety of hosts they may attack, ranging from monophagy (specialists attacking only one species or a few closely related species) through oligophagy to polyphagy (generalists attacking hosts in a wide variety of taxa). This range of hosts is a continuum with few well-defined parameters (Fig. 9), and very few species are properly placed at either extreme. Nevertheless, the concept of a generalist versus a specialist plays an important role in biological control applications. (iii) Most parasitoids develop as a single individual per host; they are called solitary parasitoids. When two or more larvae can successfully develop in a single host, they are called gregarious parasitoids. The most extreme example of gregarious parasitism involves polyembryony, the production of several larvae from a single egg. Polyembryony is found in a few species of Platygastridae and Braconidae, and virtually the entire tribe of Copidosomatini (Encyrtidae), where one egg may produce up to 3,000 larvae.



Parasitic Hymenoptera (Parasitica), Figure 8 **Adult of *Agathis gibbosas* (Say) (Hymenoptera: Braconidae) (from USDA).**



Parasitic Hymenoptera (Parasitica), Figure 9 **Adult of *Pteromalus eurymi* Gahan (Hymenoptera: Pteromalidae) (from USDA).**

(iv) Parasitoids also can be classified by the stage of host attacked and the span of host stages during parasitoid development, e.g., egg, egg-larval, egg-pupal, larval, larval-pupal, etc. (v) When a host is killed without undergoing further development, the parasitoid is classified as an idiobiont. Conversely, koinobiont parasitoids allow their hosts to continue developing after the initial parasitism, thus ultimately providing a larger food source for their larvae. (vi) Parasitoids which do not attack other parasitoids are primary parasitoids; those which develop at the expense of other parasitoids (exclusive of those which may kill competing parasitoids but do not rely upon them for development) are hyperparasitoids. Hyperparasitism can be obligate or facultative. Most hyperparasitoids attack primary parasitoids and are called secondary parasitoids, but tertiary and even quaternary parasitoids can occur facultatively. Hyperparasitoids which attack their definitive host after it has killed its own host may be referred to as pseudohyperparasitoids. Finally, an unusual form, heteronomous hyperparasitism, occurs in a few Aphelinidae; in these species the females always develop as primary endoparasitoids of scales or whiteflies, but the conspecific males can develop in several different ways: as diphagous parasitoids (primary ectoparasitoids of the same host), as heteronomous hyperparasitoids (obligate or facultative hyperparasitoids on their own [= autoparasitism] on other species), or remarkably, as heterotrophic parasitoids (primary parasitoids of Lepidoptera eggs).

Hosts have evolved several lines of defense against parasitism, using morphological, behavioral and physiological adaptations. Chief among the latter is the encapsulation of foreign objects mediated by haemocytes. Endoparasitoids in return have developed several strategies to ensure their success, including: (i) avoidance by oviposition into specific sites of the host not accessible to its hemocytes; (ii) attack though the injection of viruses, teratocytes (=giant cells, trophic cells or trophoserosa cells), or venom along with the egg; and (iii) passive defense through morphological adapations of the egg which inhibit encapsulation.

The primary source of nutrition for parasitoids is the host of the larva. However, many species also feed as adults to maximize their reproductive capacity and life-span, typically feeding on honeydew, nectar and other plant secretions. Additionally, the females of many species will feed on the hosts as well (host-feeding), in some cases leading to the death of the host.

Although most of the Parasitica are true parasitoids, in some groups a single larva will feed on a number of prey found in an enclosed area (typically an egg mass or several small larvae in a gall or cell), and thus are actually predators. In a few groups (Agaonidae, Eurytomidae, Pteromalidae, Torymidae, Tanaostigmidae, Eulophidae, Braconidae, Cynipidae, and Platygastridae) there have been revisions to phytophagy, in many cases marked by gall formation.

Adults have developed some remarkable abilities to parasitize otherwise protected hosts. Two species (a mymarid and a trichogrammatid) are fully aquatic, using their wings and legs as oars, while an ichneumonid species can stay underwater for 30 min searching for prey. The deliberate use of another species for transport is termed phoresy, and several Parasitica species practice it. Scelionid and trichogrammatid females will ride on the female adult of their hosts, so that they may immediately parasitize newly laid eggs. Phoresy has also been recorded in the Torymidae and Pteromalidae.

Biological Control

In biological control programs, it is essential to use agents which do not attack non-target organisms, and parasitoids of insect pests in general tend to be more host-specific than predators. Thus the parasitic Hymenoptera, which comprise more parasitoid species than any other group, provide the greatest pool of potential agents against insect pests. In classical biological control programs, the majority of successes have been through importations of agents from three parasitic families:

Aphelinidae, Encyrtidae and Braconidae. In mass-culturing and release programs, the Trichogrammatidae, Braconidae and Pteromalidae have been heavily relied on. The most important families (and some of the principal taxa of pests they are used against) are as follows:

Chalicidoidea
  Aphelinidae (Aphoidea, Diaspidae, Aleyrodidae and Lepidoptera)
  Encyrtidae (Pseudococcidae and Coccidae)
  Trichogramatidae (Lepidoptera)
  Eulophidae (Chrysomelidae and Lepidoptera)
  Mymaridae (Cicadellidae)
  Pteromalidae (Muscidae)
Ichneumonoidea
  Braconidae (Aphoidea, Lepidoptera and Tephritidae)
  Ichneumonidae (Lepidoptera and Curculionidae)
Platygastroidea
  Scelionidae (Pentatomidae and Noctuidae)
  Platygastridae (Aleyrodidae)

Fossil Parasitica

The parasitica appear to have arisen in the Jurassic Period, based on the fossil remains from that time of 13 extinct families reputably assignable to the group. By the Cretaceous period, several modern families had appeared, while almost every extant family is known from the oligocene period. Parasitic Hymenoptera fossils are known from both amber and sedimentary deposits, and from Australia, Asia, Europe and North and South America.

► Wasps, Ants Bees and Sawflies

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Parasitic Wood Wasps

Members of the family Orussidae (order Hymenoptera: suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Parasitism

Living on or in another organism, and using that host to obtain food. The parasitic relationship is usually debilitating for the host, and sometimes fatal, though fatal conditions are perhaps more correctly termed parasitoidism.

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina

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Pampean grasslands were dramatically modified after the introduction of exotic plant species for livestock industry and agriculture during the last century. A succession of wheat, maize, linseed, green pastures (mainly alfalfa and clover), sunflower, grain sorghum, and lastly soybean crops have changed the original grassland community structure and function. To date, the landscape in the Pampas comprises an assortment of secondary natural grasslands, and farming and crop fields with differential degrees of disturbance (i.e., use of agrochemical, planting techniques, etc.). Soybean and wheat are the major summer and winter crops, respectively. Extensive cropping and grazing are dominant practices, but allocation of land for each fluctuates according to changes in market demand and technology. Relicts of native plus introduced flora and fauna can be found in small areas of abandoned land, and in corridors alongside roads and railways. Together they cover a significant proportion of the pampean landscape.

Most regions of the world suffer the effects of invasions by introduced crops. In the case of insect communities, crops are colonized by herbivorous species; the recruitment is influenced by the natural reservoir of fauna associated with native (wild) plants chemotaxonomically related to that exotic crop, as well as by the deficiency of a broad spectrum of defensive allomones that make plants vulnerable.

Predators, parasitoids and pathogens attack herbivorous insects. Parasitoid insects are defined as entomophagous insects. Parasitoid larval stages feed internally (endoparasitoid) or externally (ectoparasitoid) upon arthropods, usually other insects, killing their hosts. One or more individuals can be obtained from a single host (solitary, gregarious or embryonic parasitoids). Parasitoids can attack a taxonomically broad range of insect orders and all developmental stages, and they themselves often are subject to attack by parasitoids; thus, they can be distinguished as primary, secondary or hyperparasitoids. Given their importance and ubiquity (probably over 1 million species), and because they can play a critical role in limiting the abundance of their hosts, parasitoids are considered to be very reliable candidates for biological control of pests.

Unfortunately, changes in natural insect communities during the agricultural expansion in the Pampas are poorly documented. However, it is interesting to investigate current insect complexes in a landscape scale, and to examine both historical and ecological processes. Insect community structure, life cycles, and interactions allow reconstruction of part of the past native communities and enable us to understand contemporary dispersion and refuges of insects in the region. It also indicates the potential use of natural enemies in the context of the biological control of pests through conservation tactics.

Larval stage of Lepidoptera naturally supports a large number of parasitoids, and non-crop habitats associated with agricultural fields provide these and other beneficial arthropods with alternate hosts or prey, food and water resources, shelter, favorable microclimates, overwintering sites, mates and refuges from pesticides.

In crops such as soybean, sunflower, alfalfa and mixed clover-grass pastures, and in monospecific patches of *Melilotus alba* L. and *Galega officinalis* L., two naturally occurring legumes alongside roads and railroads, and in crop borders in the northwest of Buenos Aires province (34°4' S, 58–60°00' W), a total of 28 Lepidoptera defoliator species can be found. These species are polyphagous and multivoltine, some are migratory and some may hibernate or overwinter. They belong to the following families: Noctuidae (21 species), Pyralidae and Geometridae (2 species each), and Tortricidae, Pieridae and Arctiidae (1 species each). Soybean supports 10 species, pastures 9, legume patches 8, and sunflower crop only 2.

Rachiplusia nu Guenée (Noctuidae) is the dominant species, being recovered from all six habitats; *Paracles vulpina* (Hübner) (Noctuidae) is found in four (both pastures and non-crops); and *Colias lesbia* Fabricius (Pieridae), *Pseudoleucania minna* (Butler), Faronta albina (Hübner) (Noctuidae) and *Spilosoma virginica* (Fabricius) (Arctiidae) in three (soybean, and both pastures; alfalfa, clover and *G. officinalis*; and soybean, sunflower and *G. officinalis*, respectively). But in general, most species are observed in one or two out of six plant habitats.

Numerous parasitoid species attack the larval stage of defoliators of soybean. Nine out of ten host species are attacked at least by one primary endoparasitoid species; all categorized as koinobionts (parasitoids associated with exposed hosts and which permit them to continue to move, feed and defend themselves). Hyperparasitoids are not found. The parasitoid assemblage comprises 30 species; they belong to Hymenoptera (4 families, 17 species) and Diptera (1 family, 13 species). *Campoletis grioti*, *Copidosoma floridanum*, *Cotesia marginiventris*, *Rogas nigriceps*, *Voria ruralis*, *Cotesia* spp., *Microgaster* spp., and *Chetogena* spp. are the most common species. Most species are solitary, some gregarious, and one polyembrionic. The number of parasitoid species attacking each host is different, highest for *R. nu* (11) and lower for *Eulia loxonepes* and *Elasmopalpus lignosellus* (1). Likewise, differences are found in parasitoid abundance (number of individuals) when comparing host species; in particular for *R. nu*, the high number of parasitoid species and number of individuals reveal the importance of parasitoids as mortality agents and point out for their preservation in protected areas. When parasitoid guild analysis is used to explore the determinants of species richness and structure of parasitoid complexes, it can be observed that the number of parasitoid guilds differs among hosts: four parasitoid guilds were recorded for *R. nu*: egg-prepupal, early larval, late larval, and larval-pupal; two for *S. virginica*: late larval, and larval-pupal, and *C. lesbia*: early larval and larval-pupal; and one for *A. gemmatalis* and *L. biffidalis*: early larval. *Elasmopalpus lignosellus* and *E. loxonepes* are parasitized by one species each (*C. marginiventris* and *Apanteles* or *Cotesia* sp., respectively).

Parasitoid assemblages from each host differ in species composition, levels of parasitism and number of guilds. Besides historical processes, some of these differences could be associated to ecological factors, such as host

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 3 Lepidoptera species inhabiting crops and corridor vegetation in northwest Buenos Aires Province, Pampean region, Argentina

Habitat plants	Lepidoptera species
Soybean	*Anticarsia gemmatalis* (Hübner), *Heliothis* spp. complex, and *Spodoptera frugiperda* (J.E. Smith), *Rachiplusia* nu (Guenée), and *S. ornithogalli* (Guenée) (Noctuidae), *Elasmopalpus lignosellus* Zeller *and Loxostege biffidalis* (Fabricius) (Pyralidae), *Colias lesbia* (Fabricius) (Pieridae), *Eulia loxonepes* Meyrick (Tortricidae), *Spilosoma virginica* (Fabricius) (Arctiidae)
Sunflower	*R. nu, S. virginica*
Alfalfa	*Paracles vulpina* (Hübner), *Leucania jaliscana* Schaus, and *Pseudoleucania minna* (Butler) (Noctuidae), *R. nu, C. lesbia*, 1 unidentified species (Geometridae), 3 unidentified species (Noctuidae)
Mixed – Clover	*Faronta albilinea* (Hübner), and *Mocis phasianioides* (Guenée) (Noctuidae), *P. minna, R. nu, C. lesbia, P. vulpina*, 3 unidentified species (Noctuidae)
M. alba	*R. nu, P. vulpina, F. albilinea, S. virginica,* 3 unidentified species (Noctuidae), 1 unidentified species (Geometridae)
G. officinalis	*Elaphia repanda* (Schaus), and *Helicoverpa gelotopoeon* (Dyar) (Noctuidae), *P. minna, M. phasianoides, S. virginica, F. albilinea, R. nu, P. vulpine*

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 4 **The parasitoid complex of defoliator Lepidoptera species on soybean crops in northwest Buenos Aires Province, Pampean region, Argentina**

Hosts					
Parasitoid complex	*R. nu*	*A. gemmatalis*	*S. virginica*	*C. lesbia*	*L. biffidalis*
Egg prepupal endoparasitoids					
Encyrtidae					
Copidosoma floridanum	x				
Early larval endoparasitoids					
Braconidae					
Apanteles lesbiae				x	
Apanteles or Cotesia sp.					
Cotesia marginiventris	x				
Cotesia a					
Cotesia b			x		
Meteorus rubens		x			x
Microgaster a	x				
Microgaster b					
Rogas nigriceps	x				
Ichneumonidae					
Campoletis grioti	x				
Campoletis a	x				
Campoletis b					
Campoletis c					
Hymenoptera					
Unidentified sp. 1					
Unidentified sp. 2					x
Late larval endoparasitoids					
Tachinidae					
Voria ruralis complex	x				
Chetogena a and *Lespezia aletie*			x		
Patelloa similis and *Lespezia* sp.			x		
Sturmia sp.			x		
Unidentified sp. 3	x				

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 4 The parasitoid complex of defoliator Lepidoptera species on soybean crops in Northwest Buenos Aires Province, Pampean region, Argentina (Continued)

Hosts					
Parasitoid complex	*R. nu*	*A. gemmatalis*	*S. virginica*	*C. lesbia*	*L. biffidalis*
Unidentified sp. 4	x				
Unidentified sp. 5			x		
Chetogena c				x	
Larval-pupal endoparasitoids					
Tachinidae					
Winthemia sp.	x				
Chetogena b			x		

abundance patterns, including constancy and predictability in time and space.

Rachiplusia nu has the most complex parasitoid assemblage, and this could be explained by its higher abundance and constancy than the other host species, and the development of two generations within the crop cycle. We might expect to find more similarity in parasitoid assemblages between *R. nu* and *A. gemmatalis*, considering they belong to the same family. However, *A. gemmatalis*, a tropical species, is possibly in the limit of its geographical distribution, having one generation a year at the end of the crop cycle and sporadic occurrence in the study area. Its lower predictability, compared to *R. nu*, could account, at least to some extent, for the observed differences. The fact that *S. virginica* does not support parasitoid guilds composed of hymenopteran species could be attributed to the long setae in the host body that, in general, would prevent the attack of wasps lacking a long ovipositor, but not for tachinids, since they can lay eggs in foliage or attach eggs on the host integument. The simplicity of the parasitoid guild structure associated with *C. lesbia* and *L. biffidalis* could be related to their low abundance.

From a regional perspective, *R. nu* population abundance is higher in summer crops, followed by multi annual crops and lower in non-crop habitats, though some low densities are registered for alfalfa and mixed clover-grass pastures. *Rachiplusia nu* larvae support 18 primary endoparasitoid species in plant habitats other than soybean, including two hyperparasitoids species registered in sunflower crops. Comparatively, the number of parasitoid species and the number of parasitized hosts is greater in crop than in noncrop habitats, ranging from 11 in sunflower (as in soybean) to four in *G. officinalis* and *M. albus*. Some species are coincidental with those registered for the soybean crop. *Copidosoma floridanum*, *R. nigriceps*, and *V. ruralis* again are the species consistently reared in five plant habitats, whereas *Casinaria* sp. is found for the first time for *R. nu* and in the five sites. The most frequently abundant parasitoid species in crop habitats is *C. floridanum*; the remaining species have lower incidence on *R. nu*. The parasitism in noncultivated habitats is very low.

Parasitoid guild analysis yields differences for *R. nu* parasitoid assemblages among plant habitats: four parasitoid guilds are found in sunflower and in soybean (egg-prepupal, early larval, late larval and larval pupal); three in mixed clover-grass, alfalfa and *M. albus* (egg-prepupal, early larval, and late larval), and two in *G. officinalis* (early larval and late larval) (Fig. 10).

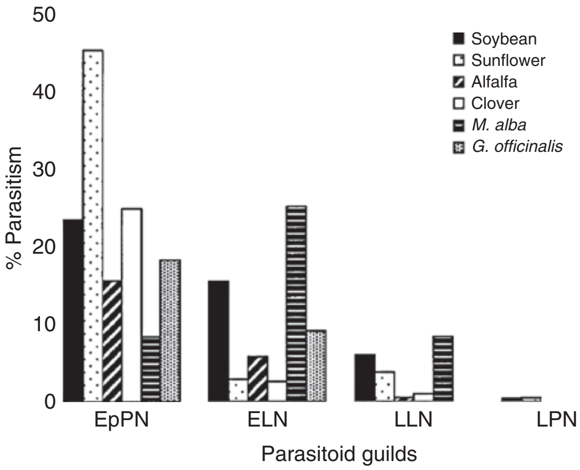
Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 5 **The parasitoid complex of *R. nu* larvae on crops and corridor vegetation in northwest Buenos Aires Province, Pampean region, Argentina**

Plant habitats					
Parasitoid complex	**Sunflower**	**Alfalfa**	**Clover**	***M. alba***	***G. officinalis***
Egg prepupal endoparasitoids					
Encyrtidae					
Copidosoma floridanum	x	x	x	x	x
Early larval endoparasitoids					
Braconidae					
Cotesia marginiventris		x			
Microgaster sp.	x	x	x		x
Rogas nigriceps	x	x	x		x
Rogas sp.		x			
Ichneumonidae					
Campoletis grioti	x	x			
Campoletis d	x				
Campoletis e			x		x
Casinaria sp.	x	x	x	x	x
Hymenoptera					
Unidentified sp. 6[a]	x				
Unidentified sp. 7[a]	x				
Unidentified sp. 8				x	
Unidentified sp. 9[b]					x
Late larval endoparasitoids					
Tachinidae					
Voria ruralis complex	x		x		x
Unidentified sp. 10[a]	x				
Unidentified sp. 11[a]		x			
Unidentified sp. 12[b]				x	
Larval-pupal endoparasitoids					
Tachinidae					
Winthemia sp.	x				
Hyperparasitoids					
Chalcididae					
Unidentified sp. 13	x				

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 5 **The parasitoid complex of *R. nu* larvae on crops and corridor vegetation in northwest Buenos Aires Province, Pampean region, Argentina (Continued)**

Plant habitats					
Parasitoid complex	**Sunflower**	**Alfalfa**	**Clover**	***M. alba***	***G. officinalis***
from *Casinaria* sp.)					
Unidentified sp. 14	x				
(from Tachinidae)					

[a] only the pupa was obtained
[b] only larvae were obtained



Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Figure 10 **A comparison of levels of parasitism for the four larval parasitoid guilds associated with *Rachiplusia nu* (Guenée) (Lepidoptera: Noctuidae) in six Pampean plant habitats (Argentina).**

In this region, only four out of seven potential parasitoid guilds defined for Lepidoptera are recorded, suggesting that potential host niches are not totally utilized. Parasitoid species belonging to guilds that attack earlier host stages are responsible for higher levels of parasitism than those attacking later developmental stages. At present, Lepidoptera defoliators occur infrequently at damaging levels and only in limited areas. The action of parasitoids seems to be, in part, responsible for maintaining defoliator populations in crops at low levels.

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Parasitization

Parasitism. This is not a widely accepted term.

Parasitoid

A parasite that kills its host at about the time the parasite completes it development.

Parasitoidism

Parasitism resulting in death of the host. This is not a widely accepted term.

Parasocial Behavior

A level of social behavior less developed than eusocial behavior. This type of sociality includes cooperative behaviors within the same generation of insects, namely communal, quasisocial, and semisocial behavior.

- ► Solitary
- ► Subsocial
- ► Communal
- ► Quasisocial
- ► Semisocial
- ► Eusocial Behavior
- ► Sociality in Insects

Parasporal Body

A particle which lies alongside the spore or is included in the sporangium along with the spore, formed during sporulation of a number of *Bacillus* and *Paenibacillus* species. If the inclusion is a crystalloid, the species is called crystalliferous. It is usually diamond-shaped (bipyramidal). When digested it releases an endotoxin.

Paratype

Any specimen in the series from which the species description was completed, other than the holotype specimen.

Parental Care In Heteroptera (Hemiptera: Prosorhynche)

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The term “parental care” refers to the set of activities that parents carry out to provide protection to their offspring. In the Heteroptera it was first described in the acanthosomatid *Elasmucha grisea* by Adolph Modeer in 1764. It is known to occur in four infraorders and 14 families, and possibly it is an ancestral character that appeared early by convergence, later to be replaced by less costly behaviors. Species providing parental care are called “social” species, and those that do not called “asocial.” Generally with social insects, brood caring is exerted by the mother because she is the sex that invests the most in her descendants and because she is certain of her maternity. Under these conditions, the investment she makes in brood caring is compensated for by her increased reproductive fitness. As it will be explained later, however, Heteroptera do not conform to this hypothesis. Also, the male usually does not cooperate in brood caring, although there are remarkable exceptions. The male bases his reproductive fitness on promiscuity. Parental care in Heteroptera poses some evolutionary dilemmas, because investment by parents in brood care reduces the fecundity of parents, and does not always enhance survival of offspring. Thus, this is not widespread in Hemiptera.

Models of Parental Care in the Heteroptera

The simplest expression of parental care is to take care of the clutch, laying it in protected places, and laying it in an environment that is favorable for the hatching young. This protection can be accompanied by aggressive behavior with respect to the predators or parasitoids that want to attack the offspring. Some morphologies favor the mechanical protection of the clutch. For example, a shield bug female can protect with her own body the clutch she lays on the ground. When moving to vegetables, the shield shape was maintained as it provides a good protection to the eggs. Later on, other means of clutch protection were developed, and the shield shape remained like a relict, although it no longer was essential for protection of the clutch. It is difficult to establish the limits of the most elaborate expression of parental care, but is usually interpreted to occur when one or both parents remain associated with their offspring, nourish them, and protect them during one or more stages of development. It can constitute the basis of incipient sociality.

Origin of Parental Care in Heteroptera

The first hemipteroid lineages appeared 260 million years ago, likely derived from scavengers that lived, fed and copulated on the ground. They moved to roots, later became predators, and finally changed to a phytophagous regime. The threat of drought and depredation in terrestrial habitats favored egg-laying in damp places on the ground, and stimulated their guarding behavior with respect to edaphic predators (as in cydnids of the subfamily Sehirinae do nowadays). When moving to aerial habitats (plants), laying clusters of eggs was retained, but the clutch was exposed to drying. The female protects her clutch to guarantee its persistence until the following generation. In order to balance the costs of this maternal protecting activity, clutches become larger-sized, but at the same time larger size made them more vulnerable to predators and parasitoids, and a positive feedback leading to establishment of parental behavior began. Only a major change in reproductive strategies allows them to escape that feedback. The clutch-protection behaviors are derived from defensive behavior (e.g., wing movement/flight behavior) and of feeding behavior that already existed in the asocial species. The aquatic habitat of Gerromorpha and the Nepomorpha reduces the dangers of desiccation and predation for these groups, and the appearance of parental behavior may be due to other factors.

Costs of Parental Care Behavior

Accomplishing the tasks of brood caring involves costs for the parent who makes them. On the one hand, the caring individual is more exposed to the attack of antagonists (e.g., the probabilities of mortality of social females of the tingid *Gargaphia* are three times higher than the mortality of asocial females). In addition, if the caring parent is female, her fecundity is reduced because, while taking care of brood, she does not lay eggs, which favors semelparity (a single act of oviposition). The total lifetime fecundity of the asocial species is significantly greater than that of the social species. For example, in *Gargaphia* the female spends more than half of her life in the care of brood, a time during which she does not proceed with another egg-laying episode. Semelparity also leads to a situation where the first, and perhaps only, clutch is much larger than that of corresponding non-nursing species. The vulnerability of the female nursemaid to predation is increased, though increase in clutch size also occurs to balance the cost of the caring behavior. In many cases brood caring is incompatible with the feeding of the parent, especially in predator species. This is of great relevance if the mother is the caring sex, as then she cannot accumulate reserves for the following clutch, thus compromising her future fecundity. Interestingly, only 10% of the Hemiptera with maternal care are predators.

Benefits of Parental Care Behavior

The benefit of parental care might be expected to result in greater survival of the offspring of the social species (Table 6). In Heteroptera, when comparing the success that parental care offers in respect to other strategies of protection, such as insertion of eggs into the vegetation or dissemination, it is not evident that caring behavior is more effective. For example, the mortality of the aggregated clutches of *Gargaphia* not being nursed is 56%, whereas in *Corytucha*, with scattered, unattended clutches the mortality is 29%. In addition, if parental care was

Parental Care In Heteroptera (Hemiptera: Prosorhynche), Table 6 **Relative protective value of hemipteran oviposition behavior**

	Protection index
Clutch size	
Eggs laid singly	5
Eggs in small groups	3
Eggs in large groups	1
Oviposition site	
On terrestrial substrate	1
On aquatic substrate	2
Elevated on stalks	3
Hidden in natural crevices	4
Glued to conspecific	5
Glued to spider web	5
Given to male for care	5
Eggs retained until hatching	5
Inserted into plant tissue	6
Protective secretion	
Eggs covered with protection secretion	2

especially beneficial and adaptive, it might appear more often in the derived species. In turn, adaptative radiation should lead to the appearance of new morphological or ethological traits (apomorphies). It might also be expected that social species are able to colonize more hostile habitats, or are more protected against attack by parasitoids or predators than those that do not take care of their offspring. However, there is no evidence to support those expectations. The groups with parental care are not the most evolved within each taxon (infraorder, family, genus), and do not differ either morphologically or ethologically from the asocial species. They do not occupy especially hostile niches either. Overall, it may be concluded that maternal care is a plesiomorphic (ancestral) character that does not require the appearance of special morphological and ethological traits. The trade-off between costs and benefits shows that it does not imply improvements for offspring fitness. Paternal care is a by-product of females abandoning brood caring, and it is only supported because males benefit reproductively from this caring behavior. Therefore, the difficulty is not to implement maternal care as a vital strategy, but rather to get rid of this expensive behavior that does not bring along with it reproductive benefits.

Replacement of Parental Care by Other Protective Strategies

The substitution of brood guarding by other means of protection has several aspects. In the first place, because it is the mother that usually performs brood caring, and is the parent that pays the greatest cost for this action, changes in her behavior tend to reduce the cost of her actions.

One strategy consists of defending the clutch only when it is in danger, making clutch defense compatible with periods of feeding by the mother. In certain species, the female protects the brood only when she is old, and chances of producing a new clutch are very low; in other words, when it turns out more beneficial to protect her (probably) last clutch rather than to abandon it to try to make another (improbable) clutch.

Another strategy is egg dumping, wherein the (dumping) female lays the eggs within or next to the clutch of another (resident or host) female, who eventually broods her own clutch and the dumped clutches simultaneously. Egg dumping has been described in the tingids *Gargaphia* sp. and *Leptobyrsa decora*, and may also occur in the coreid *Physomerus grossipes*, in the aradids *Neurocterus hochstetteri* and maybe *N. pseudonymus*, and in the reduviids *Rhynocoris carmelita* and *Pisilinus tipuliformis*. For egg dumping to arise, some prerequisites are required. First of all, maternal care is needed. Also, opportunity for iteroparity (repeated reproduction) to benefit from avoiding maternal care must exist. Good synchrony in reproduction within the species is also required in order for the dumping female to have a clutch of eggs to contribute to a receptive resident female, and also to assure that the eggs and young develop at about the same rates so the resident female will not give up protective behavior too early. Egg dumping is also facilitated if breeding individuals are aggregated, making it easier to find a host female.

The (dumper) females that transfer the care of their eggs to a (guarding) female produce a new clutch immediately, while oogenesis is suspended in guarding females. In light of the trade-off between care and future reproduction, two powerful forms of selection compete. On one hand, selection acts for protection of young; on the other, it acts against maternal behavior. The receiving female cannot easily escape her guarding role and transform into an egg layer. Immediately after egg-laying, decrease in juvenile hormone titer promotes guarding behavior, a condition that does not revert even if opportunities arise to do so. On the contrary, high juvenile hormone titer promotes oogenesis and laying, thus egg dumping. The resident female benefits from the lessened impact of parasitoids and predators on her own descendants. Resident eggs are placed in the middle of the clutch, where mortality is about 23%, whereas dumped eggs are placed peripherally (60% of perimeter eggs are dumped), where mortality is about 37%. Thus, dumped eggs provide a buffer zone of protection. Resident nymphs benefit from dilution among nymphs produced by dumper females, dilution making them perhaps less vulnerable to predators and parasitoids. A greater percentage of host offspring survives as brood size increases. Egg dumping can be said to be mutualistic between conspecific females. In fact, in the case of *G. solani*, only 10% of the females try to prevent egg dumping, and apparent attempts to attract egg dumpers have been reported. Perhaps volatiles deposited on the clutch by the host mother may be cues for dumping females. Dumper females are high-quality females, who may increase their reproductive fitness by avoiding the costs of maternal care. In *G. solani*, an increase of 20% fitness has been reported, perhaps due to higher survival rates of dumper females. To achieve benefits, a female must dump once or twice in her life. Dumping twice results in tripling of lifetime reproduction.

Forces that may have enhanced egg dumping are simple natural selection (resulting in direct benefits to fitness) and/or kin selection (indirect benefits to fitness). No mechanism of mutual recognition between relatives has been reported, but aggregation of reproductive conspecifics may increase the chances of dumping in kin clutches.

Finally, the mother can detach herself from brood caring and transfer it to the father. Since the costs of maternal care are higher in predatory species (maternal care and patrolling to hunt prey are incompatible activities), it is no wonder that the paternal care has been developed in belostomatids and reduviids, both families of predatory insects.

Other strategies have allowed some Heteroptera to avoid brood caring. A first opportunity had to be to avoid large-sized clutches, scattering them in time and space. This change was beneficial, as observed by the mortality by depredation of the clutches of *Gargaphia* (56%; large-sized clutches) and those of *Corytucha* (29%; scattered, smaller clutches). Scattered clutches are preferred, as the Piesmatidae and the Berytidae do, laying 1–3 eggs every day. Triatominae drop the eggs as they walk. In the case of massive clutches, they may be hidden, as lygeids, dipsocorids and thaumastocorids do. Protection is increased if the clutch is covered with extra secretions, as occurs in urostylids and reduviids of the subfamily Holptilinae. Oothecas can even be produced (with a shellac-like covering), as occurs in the plataspids and many reduviids of the subfamily Harpactorinae. When moving to plants, eggs may be laid on the leave or stem surface (epiphytic oviposition), and must be more resistant to desiccation by means of a thicker chorion. Those eggs may be larger and produce larger hatchlings. However, they are very attractive to the antagonists, unless they are protected. A better option is to insert eggs in plant tissues (endophytic oviposition), resulting in lower risk of mortality due to desiccation. The cost of this endophytic oviposition strategy was the reduction of egg size, which implies smaller hatchlings, but a beneficial side-effect is better protection from antagonists. An intermediate option between maternal care and asocial behavior are ovoviviparous (as is the case in some Microphysidae) or viviparous (as in some Anthocoridsae and Aradidae) strategies, which are compatible with food searching, although not with a new reproductive episode. Therefore, by means of changing the location or size of the clutch, most Heteroptera (95% of the species) have left the parental option in favor of other alternatives that protect the clutch without invoking reduced survival or fecundity.

Persistence of Maternal Care

Clearly there are alternatives to maternal care behavior. If, in spite of its disadvantages or lack of advantages, maternal behavior persists in some groups of Heteroptera, it is likely due to lack of alternatives. Maternal behavior therefore remains as a relict trait. An example of why maternal care might persist might include withering of the host plant before embryonic development has been completed, or insertion of eggs into the withered plant would not afford protection. Or, as happens in *Parastrachia japonensis*, food (fruits of *Schoepfia jasminodora*) is available only seasonally, and this factor leads inevitably to the semelparity, even if maternal care did not exist. In other words, the care of offspring does not represent any cost with respect to the future fecundity. Maternal care usually appears or is maintained with semelparity, that in turn is conditioned by diverse ecological exigencies, e.g., climate, food, mates. In these cases, reproduction happens only a few times, and it is associated with very large-sized clutches, taking advantage of the abundance of the limiting resource.

Groups That Display Maternal Care in Heteroptera

Nepomorpha: Gelastocoridae (*Nethra martini*), Gerridae (*Halobates*)

Leptopodomorpha: Saldidae (*Aepophilus*)

Cimicomorpha: Reduviidae Harpactocorinae (*Pisilus*, *Endochus*, *Rhinocoris*) and Emesinae (*Ghinallelia*); Tingidae (*Gargaphia*, *Leptobyrsa*, *Phyllomorpha*)

Pentatomorpha: Aradidae (*Mezira, Neuroctenus, Ctenoneurus, Brachyrhynchus)*; Coreidae *(Physomerus)*; Cydnidae *(Sehirus, Adomerus, Canthophorus, Tritomegas, Brachypelta, Legnotus, Parastrachia)*; Acanthosomatidae *(Anaxandra, Elasmucha, Sastragala)*; Scutelleridae *(Cantao, Augocoris, Pachycoris, Tectocoris)*; Phloeidae *(Phloea, Phloeophana)*; Dinidoridae *(Cyclopelta)*; Tessaratomidae *(Pygoplatys, Erga)*

Examples of Maternal Care

Tingidae

All the species of the genus *Gargaphia* (more than 60) perform maternal care and live on Solanaceae. The mother watches the egg clutches. The nymphs seek an unopened leaf, where they take refuge. When predators (e.g., nabids) approach, the mother faces them, extending and raising the wings. The mother may even perish in this defensive act. *Gargaphia solani*, after copulation, performs egg-laying over a period of about a day and a half on the lower surface of the foliage. Altogether she lays more than 100 eggs. The female protects her offspring until they reach maturity, and she accompanies them when they move to look for new food and refuge. The mother prevents the fragmentation of the group by directing all brood into a compact group. This behavior allows 30% of the descendants to reach the adult stage, as opposed to 3% of other genera of the same family which do not take care of brood. Genus *Leptobyrsa* performs a very similar maternal care.

The case of *Phyllomorpha laciniata* (golden egg bug) is somewhat controversial. Adults carry eggs on their backs. Males, in fact, carry double the number of eggs that are carried by a female.

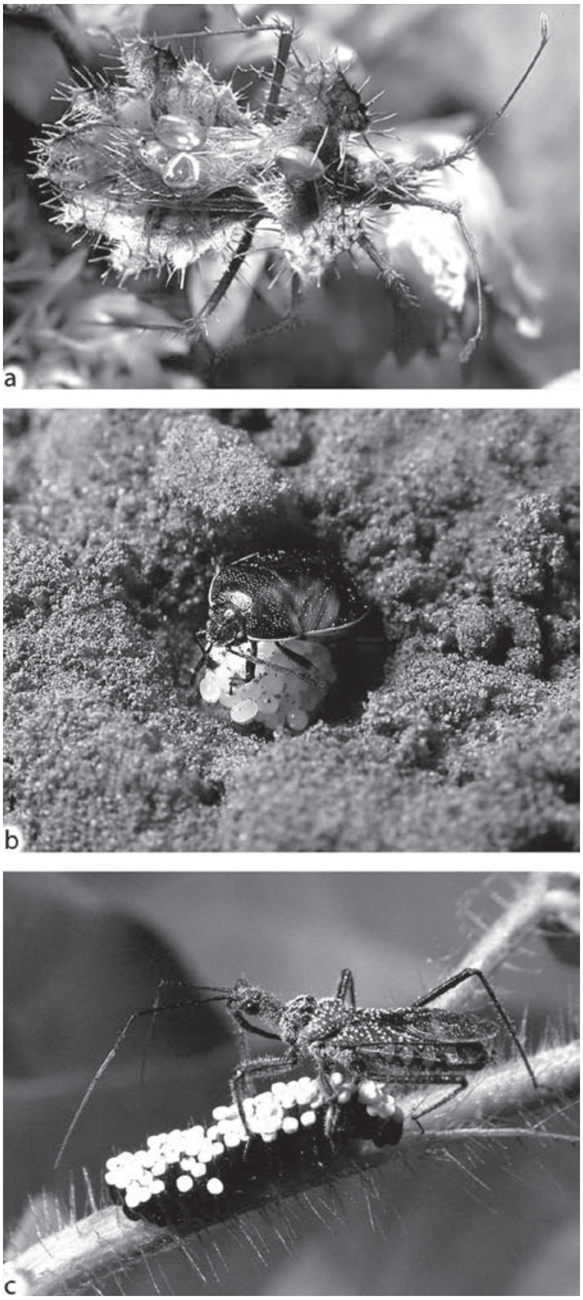
Phyllomorpha laciniata populations have a sex-ratio that is male-biased. Copulation is quite arduous (20 h under laboratory conditions), and afterwards the male stays with the female to prevent her from future copulations. During that entire period of time, males cannot avoid the gravid females that desire to lay their eggs on his back. Also females may have to tolerate gravid females gluing eggs on their backs. As the egg-carrying male does not modify his behavior, some authors do not consider the case of *P. laciniata* an example of paternal care. Rather it would be a maternal strategy, because her clutch obtains additional care when affixed to the back of conspecifics, either males or females. The ovipositing female benefits, of course, by being freed of brood caring. In this case, it may be that the males are victims of social parasitism inflicted on them by egg-laying females, and back-brooding is the price he must pay to keep a mate. This would be the case also of the gerrid *Halobates* and the reduviid *Stenolemus arachniphagus*, as they also display male back-brooding.

Coreidae

The female of *Physomerus grossipes* keeps large-sized clutches stuck to vegetation. She gives the offspring predigested food, and also the symbiotic microorganisms they will need in the future.

Cydnidae

The simplest form of protection is that the female places the clutch in cracks in the soil and watches them (Fig. 11). However, in some cases, the behavior is more complex. *Parastrachia japonica* lives in laurisilva (laurel) forests, and congregates in short trees of different genera, forming groups of up to 4,000 individuals. The fertilized females usually move away from the group (moving up to 2 km) before locating a small depression in the litter (she also may excavate this depression) which may



Parental Care In Heteroptera (Hemiptera: Prosorhynche), Figure 11 **Parental behavior in Heteroptera: (a) Golden egg bug, *Phyllomorpha laciniata* (Hemiptera: Coreidae) with eggs carried on its back (photo courtesy of Arja Kaitala); (b) egg guarding by *Sehirus cinctus* (Cydnidae); (c) egg guarding by *Rhinocoris tristis* (Reduviidae) (photos b and c courtesy of Doug Tallamy, University of Delaware).**

serve as an oviposition site. The eggs of the clutch are glued together, and in case of danger they may be transported by the mother with the aid of the tip of the rostrum ("rostripulation") beneath her body. If the danger increases, the female will try to drive away the predator. The mother protects the offspring until they reach the third instar. In addition, the female actively provides food to her brood. With the tip of rostrum, she gathers the falling fruits (drupes) of *Schoepfia jasminodora*, which are inaccessible to the nymphs. She moves the drupes to the developing nymphs, who congregate in numbers from 2 to 10 per drupe. It appears that collective enzyme injection by the nymphs is the only way to soften the interior of the drupes and allow ingestion. The females of *Legnotus limbatus*, *Sehirus bicolor* and *Sehirus nievimarginatus* also rostripulate the clutch, and they protect the young until the second instar.

Acanthosomatidae

Usually, maternal care consists of protecting large-sized clutches stuck to the leaves (Fig. 12). The female of *Elasmucha grisea* (parent bug) locates herself on the clutch (40–50 eggs) and protects it with her own body, without abandoning it even to feed herself. The care can be prolonged until the third instar, but by this time the mother remains beside the offspring, because they are too big to be shielded. The nymphs tend to aggregate, which facilitates maternal care. *Elasmucha grisea* can be considered a subsocial species, because the females often nurse their young collectively. This shared guarding behavior induces greater clutch size. In addition, the survival of the offspring is increased two-fold. The negative aspect of the shared guarding behavior is that the group becomes more tempting to insectivorous birds. This may explain why this behavior is observed, at most, in 30% of the females. *Elasmucha fieberi* behaves very similar to the previous species, but less is known. The female of *Elasmothetus interstinctus* protects her brood with her own body, before and after hatching, orienting herself toward the source of danger. The mother follows the movements of the brood, protecting them like an umbrella. The protection lasts only during the first instar. After the first molt, the nymphs preserve a certain gregarious instinct, but finally separate.

Phloeidae

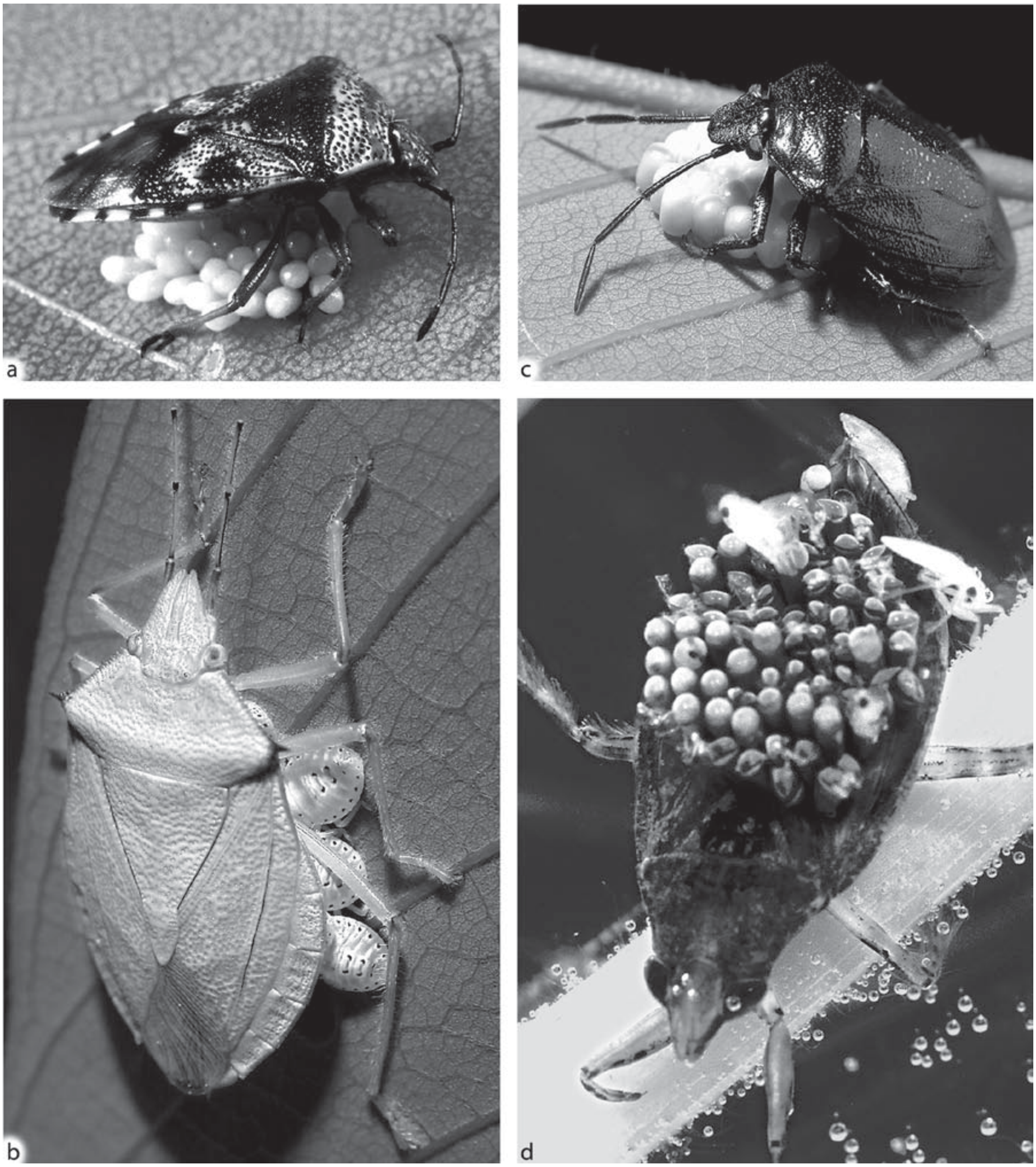
The female lays eggs in crevices of the host tree, and soon she covers the crevices with her body. The newly hatched nymphs seem to feed themselves on the mother, since their mouthparts are still too short to pierce the hard bark of the tree. In this case, the reason for maternal care is feeding, more than the protection from antagonists.

Tessaratomidae

Pygoplatys sp. and *Erga* sp. glue clutches of eggs to plants, and look after them. The female of *Pygoplatys acutus* protects, under her body, a mass of more than 30 nymphs. These attach firmly to their mother and she may even walk or fly without losing any nymphs. The mother is able to nourish herself on several plants, but not the nymphs.

Paternal Care

The concept of paternal care includes only those cases in which the father, alone or together with the female, is involved in the direct brood care, either of eggs or nymphs. It does not include cases where the father provides nuptial gifts (including spermatophores) to the future mate as prezygotic investment in the offspring. Although there have been attempts to relate paternal care to the type of fertilization, there are examples of paternal care both in species with external fertilization (when the male has greater certainty as far as his paternity) and in species with internal fertilization (as is the case in Heteroptera).



Parental Care In Heteroptera (Hemiptera: Prosorhynche), Figure 12 **More parental behavior in Heteroptera: (a) acanthosomatid guarding eggs; (b) Colombian pentatomid guarding nymphs; (c) *Antiteuchus tripterus* (Pentatomidae) guarding eggs; (d) Male *Belostoma* water bug with eggs and hatching nymphs on his back (photos courtesy of Doug Tallamy, University of Delaware).**

The transference of brood care to the male benefits the female. On the one hand, it releases her from limitations on her future fecundity, by allowing her greater freedom to feed and ability to escape predation (according to the enhanced fecundity hypothesis). On the other hand, it allows her to identify the males with better genes (handicap principle). In this second hypothesis, a male that successfully takes care of the offspring displays good genes, because the attention to brood care exposes him to greater risks than when he is not nursing the brood, just as happens in the case of maternal care. Paternal care is then a sexually selected character. The benefits of transferring brood-caring to the male are more evident in the predatory groups, where it is not possible to predate and nurse at the same time, so the female decidedly compromises her future fecundity.

Exclusive paternal care often occurs when the populations are in restricted spaces. This favors the promiscuity of the brooding male, which is constrained to a discrete space. Also, male caring behavior is frequently associated with populations in which the sex ratio is 1:1 or female-biased. If there were not selection in effect with regard to paternal behavior, it might be advantageous for the male to increase his fitness by promiscuity via scramble competition, leaving the brood unattended. On the other hand, if the density of females was very low the attachment of the male to the brood, which restricts his movement, might result in too few mating opportunities for him.

In Reduviidae it has been observed that the males are much more numerous on their host plants than the females. The time that the male remains with the offspring is directly related to the number of matings that he obtains in that place.

Often the female will choose a male that already has a clutch in his care, and the male will welcome an additional clutch and even will take care of clutches that are not his because this makes him attractive. Desire to become attractive even leads to the males robbing eggs that are being nursed by other males. An exception to this norm are Belostomatidae, in which bouts of oviposition and copulation alternate. In other words, in Belostomatidae the male makes sure that the clutch is his (natural selection). Male Belostomatinae, which are back-brooders, allow eggs that are not his, but prefer to assure their paternity. In this case the limiting factor could be the surface of the male's back. However, a Lethocerinae male, emergent-brooder (lays the clutch in the vegetation of the surroundings, a much less restricted space), willingly accepts clutches from several females, even if they haven't mated with him, because in doing so he becomes more attractive. The most difficult period for the female to choose a mate is at the beginning of the egg-laying period, when no male is protecting a clutch. The female must take considerable risk, and in case of failure (i.e., the male does not care for the offspring correctly), it may be assumed that this first clutch is only one fraction of her total fecundity. A possible signal of future good parental behavior would be the interest the male shows in receiving a clutch. Perhaps in these cases of uncertainty the first clutch is less numerous than the rest, but this has not been assessed. In the Heteroptera, the absence of activities that show the responsibility of the future father make the selection by the female more difficult.

In summary, paternal care is developed if it is compatible with male promiscuity at the same level as if the father did not take care of the offspring. This assumes that the father is associated to his offspring when they are hatched, and that paternal care is related to guaranteed paternity (both achieved as the female immediately lays eggs after mating). Paternal care is too risky not to be balanced by improved mating success associated with such behavior. Normally the caring male courts his mates where oviposition occurs, or he rides inseminated females until egg-laying occurs. Promiscuity is more common in the species with exclusive paternal care, the sex ratio is 1:1, or the population is highly female-biased. In such cases, the male becomes the limiting sex, and is sought after by the female (reversal of the typical sexual role). In addition, the females are iteroparous, and the opportunities for male promiscuity are numerous.

Groups That Display Paternal Care

Belostomatidae

In this family, exclusive paternal care is obligated, which means that in 99% of the cases, care is performed by the male. This was first observed in Belostomatinae at the beginning of twentieth century by Torre Bueno. In the fossil record, *Mesobelostomum*, a Lethocerinae from Solnhofen limestone (southern Germany), most probably brooded. Males require less food than females, predation efficiency is reduced by brooding, and females with a richer nutrition increase clutch size, so that Belostomatidae are a good example of paternal care selected by the enhanced fecundity hypothesis. Typically, bouts of copulation (up to 30) and oviposition alternate.

In *Lethocerus* (subfamily Lethocerinae), paternal care was first described in the late 1970s, and is called emergent-brooding. Sexes meet through the ripple signals performed by the male. Males that signal longer obtain more copulations than males that signal more briefly. In some species, males may also signal acoustically. Low frequency ripples may also be an attractive signal for predatory water spiders. Males may mate sequentially with several females, and their eggs will form a large egg clutch that will be attended by the polygynous father. In *Lethorecus americanus*, a male can take care of eight clutches simultaneously. The female glues the clutch in a plant stem or another emergent substrate along the pond margin. The adhesive is a hydrophilic mucopolysaccharide, which may contribute to moisture retention. It has been reported that *L. maximum* in Trinidad selects the oviposition height above water level depending on the season, higher in the rainy season. After each copulation bout, the female climbs out and lays 1–3 eggs, embedding them in a foamy substance produced by annex glands in her reproductive system. The eggs are then laid in a bubble net. When she completes her final oviposition, she abandons the clutch and never returns to it. Most probably, females never brood, because when left with no male after copulation she stops egg-laying and soon deserts her eggs, leaving the incomplete batch unattended. Laying eggs outside the water is complicated by the challenge of drought. In this case, paternal care will involve shading the clutch and periodically sprinkling it with the water that drains off his body. In very dry conditions, where water would evaporate prior to the male reaching the clutch, he imbibes water and regurgitates it onto the eggs. In *L. medius*, eggs were wetted every 30 min. Moreover, the father displays aggressively if threatened, especially against birds or any threat coming from above. Locating the clutch in the emergent substrate seems to be mediated by a scent delivered by the metathoracic scent gland system (MSGS). As the female has to track the clutch for a shorter time than males, the metathoracic scent gland system in females is much smaller than in males.

Males of Lethocerinae are not an active part of the population while nursing, and although sex ratio is nearly 1:1, the operational sex ratio is female-biased and females compete for the opposite sex. However, the wave motion the male produces to sprinkle the clutch is very similar to that produced when searching for mates. So females track this sign as to a possible mate, and as a result, brooding males do not lose chances for promiscuity, which is also reinforced by their caring behavior. If no other available mate is found, the female may attack the nursing male with the front legs and the rostrum and destroy the clutch, which stimulates a new mating. The male keeps an ambivalent attitude, because he tries to defend the old clutch and copulate with the attacking female at the same time. Only in about 30% of the cases are the caring males able to fend off the attacks by the females. Females may also drive the male away from the clutch he is caring for, copulate with him, and force him to brood the new clutch. The older nymphs of other clutches also may cannibalize eggs about to hatch. The older the clutch, the greater the amount of time the male spends next to it, seeking to avoid an encounter with a reproductive female that could spoil his investment in the brood.

Belostomatinae perform back-brooding. Courtship begins with “push-ups.” Only after one or more couplings does the male allow the female to glue the eggs on his back. As in Lethocerinae, copulations and egg-laying alternate. One to four eggs are laid per oviposition effort. Males do not copulate while an egg pad is fixed to their back, and this is a very important restriction since mating season lasts 60–90 days. Periodically, the male cleans, aerates and wets the eggs with his hind legs. In Belostomatinae, the risk is drowning, as the oxygen and carbon dioxide diffusion rates in water are not sufficient to assure survival of the clutch. To enhance gas exchange, the male floats at the surface of the water, which is a very risky behavior because while doing so he is exposed to predators. Females and unencumbered males never behave in such a way. While underwater, the male aerates the clutch through brood pumping, a behavior that increases the flow of water over the surface of eggs. Brood pumping may be a plesiomorphic (ancestral) trait, modified from display-pumping. Lastly, the male may move its hind legs to brush and circulate water over the egg clutch (brood-stroking). In this way he also keeps informed about eggs still attached to his back. It has been experimentally verified that the eggs nursed in such ways have the highest percentage of hatching, as opposed to those which remain submerged in water, above the water surface, or pass from aerial habitat to the aquatic one but without receiving greater attention. Back oviposition sites are the limiting vital resource in the belostomatine giant waterbugs. Occasionally, eggs may also be laid on the female's back.

Under stressed conditions, the male may kick off an egg clutch, leading to egg abortion. Probabilities on kicking off an egg clutch depends on clutch size and age (i.e., on the male's invested effort). Also, the egg clutch is kicked off when all eggs have hatched, which occurs about 14 days after egg-laying. Death of the clutch may also occur when the male does not emerge from the water due to threats of predation; the developing embryos drown. Oophagy arises when the probabilities of eggs hatching are very low, and with ingestion of eggs the male partly recovers the energy invested in their care. As there is no need for clutch tracking in Belostomatidae, they lack the metathoracic scent gland system.

Brood caring means an elevated cost to the male, including a greater risk of predation, a smaller probability of successful hunting or of dispersing (the eggs glued on the back immobilize the wings), and perhaps also a smaller probability of fertilizing eggs. However, the male assumes these costs because he has certainty of paternity. Indeed, he accepts the clutch laid by the female with which he has just mated, because in these species sperm precedence is the rule (last in, first out).

The enormous size of the Belostomatidae (somewhat over 110 mm) seems to be related to paternal care, a trait following ancillary selection (selected by a primary trait, which is large size). Larger size opens new opportunities for preying on vertebrates. Great size is achievable due to prolonged life cycles and additional instars. However, this is a risky option, as nymphs are unable to fly and they may need to escape from temporary ponds. Such ephemeral habitats would be more suitable for insects with rapid development. On the other hand, a life cycle with five (rarely four) molts is fixed in Heteroptera. As a consequence, the only way to reach this great size is being born of very large eggs, which carries with it the constraint of higher metabolic demand, often exceeding the gas diffusion rate in water and threatening the survival of the embryos. If egg-laying on shore is adopted, which benefits from higher gas diffusion rates, the risk of desiccation arises. Adaptation to a water habitat relaxes the need for chorion protection against drought as compared with terrestrial bugs. Belostomatid egg yolk is richer in proteins than in lipids, and more water is needed to metabolize proteins. Paternal care in Belostomatidae not only counteracts the challenges of drowning (Belostomatinae) or desiccation (Lethocerinae), which are necessary to assure embryo survival, but frees the female from those tasks and leaves her ready again for reproduction (iteroparity). Perhaps some ancestral characters produced an adaptation to emergent-brooding. This could result from alternating oviposition and copulation, with the father remaining in the vicinity of hatching eggs (initially as a postinsemination association, to prevent further couplings of the female). This could include fighting against potential predators and inhibiting cannibalism on the part of the male. Also, the eggs benefit from being removed from the water as this inhibits growth of algae and fungi, but need to be moistened periodically to avoid desiccation. The result might be the evolution of emergent-brooding from a non-brooding ancestor. Back-brooding could have been produced by accident due to absence of emergent substrates, but the adaptiveness of breathing behavior is a consideration.

Reduviidae

In *R. tristis*, the male remains on the female's back and copulates with her until egg-laying. The female glues the clutch to a leaf of a plant. As egg-laying is completed, the male begins to nurse the offspring. For a short period of time, the female will come back to copulate again with the guarding male, laying additional egg batches. Other females will approach the guarding male and will mate with him, adding more eggs to the initial clutch. Also, females who didn't mate with him are allowed to contribute to the egg mass. In *R. tristis*, it has been shown that a male may protect up to ten clutches of five different females. As long as the father is caring, he will chase off parasitic wasps and other threats, although he is not always successful. During this period he does not feed, as this would mean abandonment of the egg mass to look for prey. Several males may congregate on the same plant, but this does not harm their chances of promiscuity. On the contrary, this situation benefits both sexes. Each male can fertilize several females, and each female can successively mate and lay eggs fertilized by several males, resulting in a greater genetic variability for their offspring. It has been recently reported that if the male abandons the clutch, a contributing female (a female whose eggs are part of the defended clutch) may replace him in guarding the offspring. In *Zelus* sp., *R. albopilosus* and *R. albopunctatus*, the father also takes care of clutches from several females, with which he may or may not have mated. Males fight to control an oviposition place, waiting for the females to arrive. In *Rhinocoris*, parental care ends as soon as eggs hatch, but in *Zelus* the male remains with the young until they disperse.

Coreidae

In the males of *Plunetis yurupucu* and *P. porosus*, the clutch is glued to the ventral abdominal sclerites of the male. This location suggests something more than simple passive cooperation on the part of the male. In a single population of *Scoloposcerus uhleri* it has been observed that the males carry the clutch stuck to the back, although this is not the case with the females.

Aradidae

In the genus *Neuroctenus*, it is not certain that the female which abandons the offspring is replaced by a male. In any case, she is replaced by another adult who guards the clutch until it hatches. It could be another female, because Aradidae typically make communal clutches.

► Bugs (Hemiptera)
► Sociality of Insects
► Gregarious Behavior in Insects

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Parental Investment

Behaviors displayed by the parent insects to increase the probability that their offspring will survive and reproduce, at the expense of the parent's ability to produce more offspring. Females are considered to invest more in offspring than males. Social behavior is considered to be a high degree of parental investment because parents invest in brood care.

Parietals

The lateral areas of the insect head between the frontal and occipital areas. Each parietal consists of the antenna, compound eye, and lateral ocelli.

Parnassian Moths (Lepidoptera: Pterothysanidae)

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Parnassian moths, family Pterothysanidae, include 19 species from southern Africa (seven sp.) and Southeast Asia (12 sp.). There are two subfamilies: Pterothysaninae and Hibrildinae (the latter subfamily also considered in Eupterotidae in some classifications). The family is in the superfamily Calliduloidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (55–75 mm wingspan), with head scaling average; haustellum naked; labial palpi porrect; maxillary palpi vestigial; antennae filiform or bipectinate. Wings rounded (Fig. 13) Maculation pale and spotted, sometimes translucent (Hibrildinae); some with long hair-like setae from hindwing margin (Pterothysaninae). Adults diurnal; possibly also crepuscular. Biologies and larvae remain unknown.

Parnassian Moths (Lepidoptera: Pterothysanidae), Figure 13 Example of parnassian moths (Pterothysanidae), *Hibrildes ansorgei* Kirby from Mozambique.

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Paronellidae

A family of springtails in the order Collembola.

► Springtails

Parsimony

Events that are the result of the fewest intervening steps or processes. In systematics, evolution is assumed to proceed along the course with the fewest number of steps.

Pars Intercerebralis

The pars intercerebralis is the dorsomedial portion of the protocerebrum. The insect brain consists of the protocerebrum (the forebrain), mesocerebrum (middle brain), and tritocerebrum (hind brain). The protocerebrum innervates the eyes and ocelli.

► Nervous System

Parthenogenesis

Development from an egg that has not been fertilized. Reproduction without fertilization.

Parthenogenetic Reproduction

Asexual reproduction. (contrast with sexual reproduction).

► Parthenogenesis

Parvovirus

Parvoviruses, the smallest DNA viruses, are contained within the genera *Parvovirus*, *Erythrovirus*, *Dependovirus*, *Iteravirus*, *Contravirus*, and *Densovirus*. Members of the *Parvovirus*, *Erythrovirus*, and *Dependovirus* infect vertebrates, whereas the host range of genera *Contravirus*, *Iteravirus*, and *Densovirus* is restricted to arthropods. The dependoviruses require a helper virus for replication; the vertebrate parvoviruses and the Densovirinae are autonomous viruses. Autonomous parvoviruses replicate through a variety of double-stranded linear DNA intermediates in mitotically active host cells.The canine and human B-19 parvoviruses are simple icosahedral viruses that are constructed from 60 protein subunits or protomers that contain three structural proteins. The insect parvoviruses produce a small, non-enveloped icosahedron (20–24 nm diameter) composed of four structural polypeptides (VP1-VP4). These viruses, like other parvoviruses, possess a relatively high DNA/protein ratio (about 37%), which confers a characteristic heavy buoyant density (about 1.40 g/cm^3) in $CsCl_2$ gradients. These viruses are very stable and are resistant to exposure to pH 3–9, solvents ($CHCl_3$), and temperature (58°C, 1 h). Insect parvoviruses, like their vertebrate counterparts, replicate only in actively multiplying insect cells. The parvovirus replication takes place in the cell nucleus and is closely affiliated to cellular DNA replication events. Parvoviruses are not capable of stimulating DNA replication in resting cells; replication of these viruses requires host cells to go through the S phase. The insect parvoviruses undergo a non-lytic cycle in cell culture.

The subfamily Densovirinae (DNVs) contains members that have been isolated mainly from dipteran and lepidopteran hosts. The DNVs in the genus *Densovirus* contain a 6 kb genome which codes for structural and non-structural proteins on separate strands. Many of these viruses are polytropic and replicate in the nuclei of all insect tissues except the midgut. The *Bombyx mori* densovirus, the sole member of the genus Iteravirus, contains a smaller genome (about 5.0 kb) that codes for all proteins on one strand and is able to replicate only in midgut cells. Members of the third genus, the *Contravirus*, have been reported to cause persistent, non-lytic infections in mosquito cell lines and have been shown to be vertically transmitted in *Aedes*. These viruses possess a 4.0 kb genome and have open-reading frames (ORFs) on the plus strand and/or negative strands. The mosquito DNVs have been examined for potential vectors for the delivery and expression of foreign genes in mosquito cells. These polytropic DNVs share characteristics of both the *Densovirus* and *Iteravirus* groups. However, unlike the lepidopteran DNVs that encapsidate plus and negative strands at equal frequency, the *Aedes* DNVs encapsidate only 15% of the plus polarity strand.

The best-studied insect parvoviruses include the *Bombyx* DNVs, the causal agents of densonucleosis in the silkworm *Bombyx mori*. Two forms, DNV-1 and DNV-2, have been detected in silkworm populations. Both DNV-1 and DNV-2 replicate in the nuclei of midgut columnar cells. The DNV-1 (*Ina* isolate) induces infected midgut cells to be discharged into the gut lumen. DNV-2 infected cells are not as readily discharged as those infected with DNV-1. In nature, both DNV-1 and DNV-2 are able to cause chronic infections in larvae of the mulberry pyralid, *Glyphodes pyloalis*. More than 50% of field-collected *G. pyloalis* larvae screened with anti-DNV rabbit antisera were infected with DNV and/or the infectious flacherie virus. It is believed that this DNV overwinters in diapausing *G. pyloalis* and is transmitted to silkworms via contamination of mulberry foliage by prior generations of DNV-infected *G. pyloalis* larvae.

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Pass, Bobby Clifton

Bobby Pass was born in Blount County, Alabama, in 1931. He received his B.S. and M.S. degrees from Auburn University, and a Ph.D. from Clemson University, the latter in 1962. He immediately joined the faculty of the University of Kentucky, where he served his entire professional career. He became department chairman after only 6 years of service, and served in that capacity for 33 years. He also served as the State Entomologist of Kentucky, a regulatory position. Known for his administrative prowess, Bobby Pass had a pioneering role in the promotion of IPM. He also played a major role in Kentucky's teaching programs, and did much to enhance the University of Kentucky's reputation in entomology. He served as president of the Entomological Society of America, and was active in the regional and national society. He died on December 12, 2001, 15 years after receiving a heart transplant, making him, at that time, one of the longest-living recipients of this operation.

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Passalidae

A family of beetles (order Coleoptera). They commonly are known as bess beetles.

► Beetles

Passandridae

A family of beetles (order Coleoptera). They commonly are known as parasitic flat bark beetles.

► Beetles

Passive Dispersal

The redistribution of animals caused by external agents such as wind or movement of seeds. The small size of insects allows passive dispersal frequently (contrast with active dispersal).

Passive Flight

One form of flight, found particularly in heavy bodied species, lacks wingbeat and fails to create thrust. This is basically a gliding or parachuting form of flight. The other basic form of flight is flapping flight.

Patagium (pl., patagia)

A small flap or lobe at the anterior edge of the forewing of some insects. It is also known as the tegula.

► Wings of Insects

Patch Dynamics

The concept that communities are not homogeneous, rather consisting of a mosaic of patches, with differing rates of biotic and abiotic interactions and disturbances.

Patch, Edith Marion

Edith Patch was born at Worcester, Massachusetts, USA, on July 27, 1876. Her family moved to Minnesota in 1884, where she had ample opportunity to live with, and observe nature. She was particularly fascinated with the monarch butterfly and at an early age came to love entomology. She entered the University of Minnesota in 1897 and received her B.S. in 1901. It was here that she was introduced to aphids, a subject that came to dominate her life. Unable to gain employment because entomology was not yet regarded an appropriate field for women, she taught high school for 2 years. However, in 1903 she was invited to organize a Department of Entomology at the University of Maine. During leaves of absence from Maine she studied at Cornell University, and was granted a Ph.D. in 1911. She served as head of the entomology department at the University of Maine until her retirement in 1937. Edith Patch wrote about 80 technical publications on insects, mostly concerning aphids, but also including many of Maine's important pests. She was interested both in taxonomy and economic entomology. Among her important works were "Aphididae of Connecticut" (1923) and "Food-plant catalogue of the aphids of the world" (1938). She was especially supportive of other students and scholars, and a significant amount of her time was devoted to assisting others to learn aphidology or in identifying aphids for others. Patch also wrote about 40 popular articles on scientific topics, about 100 nature stories for children, and 17 books on natural history for children. She was elected the first woman president of the Entomological Society of America and received many other honors and recognitions associated with her expertise in aphids. She died at Orono, Maine, on September 27, 1954.

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Patchy Environment

A habitat within which occurs significant variability in suitability for an organism of interest.

Patella

In arachnids, a leg segment between the femur and the tibia.

Pathogen

A virus, bacterium, parasitic protozoan or other microorganism that causes disease by invading the body of a host; infection is not always disease because infection does not always lead to injury of the host.

Pathogenesis

The ill health or death of an organism caused by a pathogenic microorganism.

Pathogenicity

The ability of a pathogen to cause disease.

Pathogen Transmission by Arthropods

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Vector arthropods are those on, or in, which pathogenic organisms can survive and be transferred. Parasites transmitted by arthropods range widely from eukaryotes, including helminths, to prokaryotes and viruses. Some of them, for example, the sporogenic *Anthrax* bacterium (a prokaryote) and myxoplasmosis (a virus that affects rabbits) survive long enough on the mouthparts of bloodsucking insects such as horseflies and fleas that they are capable of contaminating vertebrate hosts. Regurgitation or the feces of their arthropod host disperse other pathogens that survive in the gut of non-bloodsucking insects such as cockroaches and domestic flies. Representatives of these groups are called contaminators. The efficiency of contamination depends upon the ability of the pathogenic agents to survive in, or on, the body of their temporary vector. The food of man or of animals can also be infected by pathogens transferred by these arthropods. In most cases, this type of transmission is occasional. However, for example, diarrhea agents can be transmitted in poorly managed hospitals where flies or cockroaches are abundant. There are some examples of persistent transmission. For example, the myxomatosis virus, which is capable of surviving for a long time on the mouthparts of *Spilopsyllus cuniculi* fleas, is transmitted from rabbit to rabbit by this vector only. In this case, the flea is an obligate, specific vector. However, this is an exception to the rule.

The term specific vector is mainly used to define the large group of vectors, mostly bloodsuckers, whose body provides not only a pathogen's survival, but also its propagation to the level of an invasive stage capable of infecting a vertebrate host.

Specificity of bloodsucking vectors is defined by the following criteria:

Any pathogen that consumes the energy sources accumulated by its bloodsucking host. The parasite propagates to enhance its chances of transmission.

A specific stage in the pathogen's life cycle is developed inside the arthropod host. This developmental stage can be distinguished morphologically (helminths, Protozoa, agent of plague) or antigenically (bacteria, viruses) or genetically using PCR for DNA/RNA identification (all pathogens).

Highly efficient mechanisms of transmission through injection or other specific contamination are characteristic.

The pathogen transmitted is relatively harmless to the vector either at the individual or at the population level.

It possesses both a) an adequate level of pathogen for the vector to be infected on a vertebrate host, and b) the ability for vector infection on an aviremic host. (An aviremic host is one that is tolerant to infection or it develops the infection much later than bloodsuckers are able to exchange the pathogen between infected and naive specimens).

The malaria agent *Plasmodium* is the best example of items 1 and 2. Only sexual forms that are not very abundant in the host blood can develop in the mosquito host. In the sporocysts of *Plasmodium*, the numbers increase a thousand-fold. Individual sporozoites flooding out with mosquito saliva can infect a vertebrate host.

There are many mechanisms of parasite transmission. The most widespread mechanism is pathogen transmission through the bite of a bloodsucker (Fig. 14). Pathogens are transmitted in the ectoparasite's saliva. All mites and ticks, mosquitoes, gnats, sand flies and tsetse flies demonstrate this mechanism of transmission. Helminthes infest the host during the bite of a fly, but not with saliva. Using their "knife and scissors" mouthpart they are able to perforate the bloodsucker's soft labium that remains in tight contact with the wound they make in the host. Passive specific contamination is typical of triatomid bugs, also called "kissing bugs" because they often sting a sleeping person's mouth where the skin is thin. Their feces infected by the Chagas disease agent are dropped over a small wound made by the bug's "dagger-like" mouthparts. Lice-borne pathogens contaminate scratches in human skin either with infected feces or with crushed louse bodies whose guts are full of *Rickettsia* (red typhus) agents. Louse saliva is a highly itchy substance and stimulates both the scratching and the subsequent lice crushing. Bugs and lice are, therefore, not only specific hosts, but specific contaminators also.

The mouthparts of ectoparasitic mites, ticks and insects are highly varied in construction, but invariably well adapted to blood sucking. The stiff "daggers and scissors" of a horse-flea's mouthparts enable rapid blood-sucking in spite of the rough skin of its host. The fine, delicate vein-opening apparatus of sand flies account for their Latin name, Phlebotominae, "phlebo-tomeo" meaning "vein dissection." The long, sword-like, flexible, often serrate mouthparts of mosquitoes and fleas enable them not only to pierce the host's skin, but also to penetrate the blood vessels. The rough, scissors-like tick chelicerae provide a relatively large hole in the host skin, inside which the hooked hypostome is inserted to ensure tick attachment. Very often, a special kind of saliva, which hardens in contact with air and is thus termed cement, anchors the tick mouthparts in the skin. This is necessary to fix a hard tick whose feeding takes several days. Saliva of bloodsucking arthropods is rightly called a pharmacological laboratory, as it either serves to irritate the host skin (lice) or to anesthetize the place of the bite (triatomid bugs, ticks and mites), or to dilate host's blood vessels and suppress blood clotting. Tick saliva is perhaps the most multifunctional in suppressing not only blood clotting, but also host immune reactions. The more detailed the study of bloodsuckers' saliva, the more diverse are the features disclosed. The presence of specific insect- or tick-borne pathogens not only alters arthropod host behavior (e.g., tick-borne encephalitis virus enhances the vector's locomotor activity) but also its saliva. For example, the malaria agent appears to disable the production of the enzyme apyrase by the mosquito salivary glands. As a result, the duration of bloodsucking is extended, and a considerable increase in sporozoite transmission to the vertebrate host is observed.

Blood consumption from vertebrate hosts is an absolute prerequisite to survival of bloodsucking arthropods. Yet, blood is the main, but not the only, pathway of pathogen transmission. Devouring the gut content of older individuals is relatively common among bloodsuckers. For example, the larvae and nymphs of triatomid bugs very often behave as cannibals, piercing the body of adults and sucking their blood content, which might be infected by *Trypanosoma cruzi*. Sucking the adult feces is also typical of these contaminators. Four pathways of pathogen transmission can be seen in this picture: two types of contamination (both from and to, the insect) and two routes of pathogen acquisition (with blood of a vertebrate or an invertebrate host) (Fig. 14).

Often enough, subadults of soft ticks suck the gut content of older individuals which have fed, thus engulfing relapsing tick fever pathogens (e.g., *Borrelia duttoni*). Likewise, there are several modes of transmission and circulation of the plague agent *Yersenia pestis* (Fig. 15) which is usually transmitted through a flea bite (donor rodent - to flea - to recipient rodent). However, it can also be acquired by the direct contact of a healthy person with an ill one in cases of the pulmonary form of the disease, or, carried from a bloodfed, infected, soft tick to a hungry flea. At present, a telluric way of plague agent maintenance is in debate. *Yersenia pestis* pathogens can be preserved and are capable of re-entering the animal/flea circle at a later time. *Anthrax* bacilli in the spore form can remain preserved in the soil for decades and then infect wild animals or livestock.

Pathogen Transmission by Arthropods, Figure 14 **Specific contamination and cannibalistic routes of Chagas disease agent. I – specific contamination: infected feces contaminate the wound made by the bug; II – cannibalistic route: hungry nymph consumes trypanosomes from the fed adult's gut; III – contamination route: hungry nymph consumes agent from the drop of fresh feces with trypanosomes.**

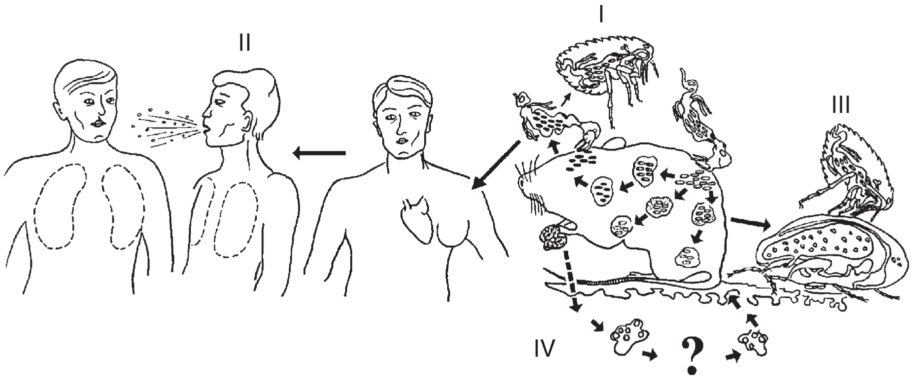
Anthrax kills the vertebrate host while horse flies feeding on the dying or freshly dead animals may disseminate this agent as contaminators. Horse flies carry the spores on their mouthparts. Even a typical vector-borne pathogen such as the malaria agent can circulate by transmission from an infected mother to a child or from an infected person to a healthy one by blood transfusion. In these cases, asexual forms of the parasite are transmitted.

The pathways of tick-borne pathogen transmission seem the most complex. The most studied examples concern the tick-borne encephalitis virus, an agent that is the most dangerous to man.

The first, "classical" pathway demonstrates infected blood consumption by an adult female tick feeding on a vertebrate showing viremia (high concentrations of the virus in host blood). For a long time, this pathway was believed to be the main one. It includes:

Transovarial transmission, implying infected blood consumption and pathogen transmission to the egg (beginning of the F1 progeny). Transovarial virus transmission has also been proven for Diptera: mosquitoes as vectors of yellow and dengue fevers, and sand flies as vectors of phleboviruses (for example, papattasi fever).

Transphasic transmission must include at least one of the following steps: transmission of a pathogen from fed and infected larvae to nymphs; survival



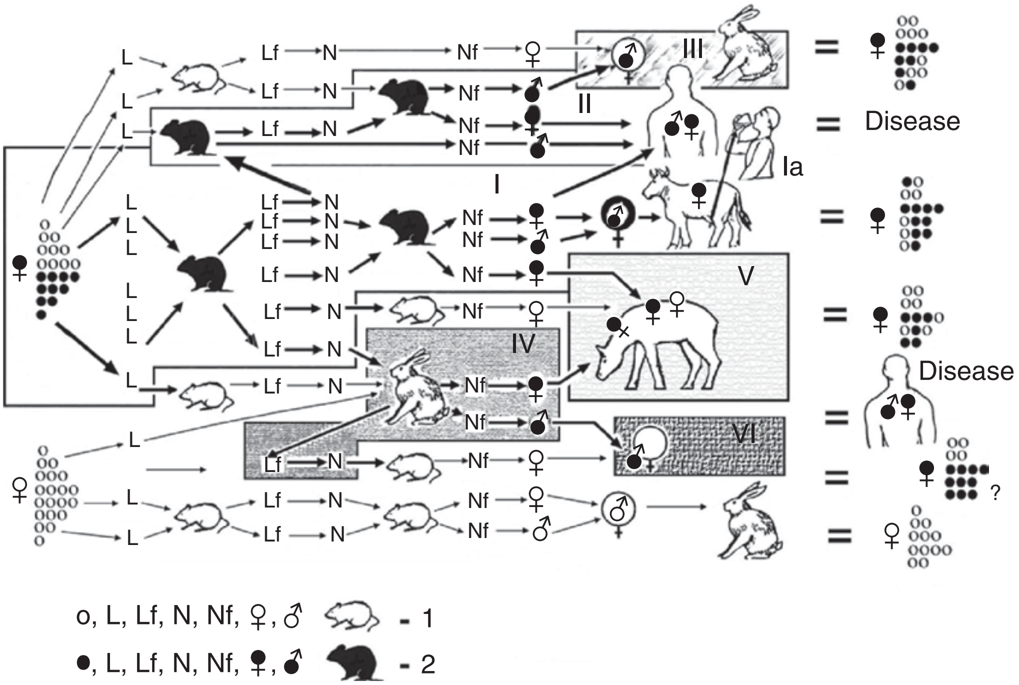
Pathogen Transmission by Arthropods, Figure 15 **Plague agent routes of transmission and circulation. I – system: flea, *Yersenia pestis* and susceptible rodent; II – generalized and aerial forms of plague; III – *Ornithodoros* as a "living can" of *Y. pestis* for fleas; IV – possible phytophase of the *Y. pestis* cycle (telluric hypothesis).**

of the pathogen in hungry and fed nymphs and its transmission to adults following the nymph's molt. Adults can transmit the virus to humans and animals. Transphasic transmission is also typical of *Borrelia*, the relapsing tick fever agent transmitted by soft ticks, and of the Lyme disease agent transmitted by hard ticks of the genus *Ixodes*.

The sexual transmission of tick-borne encephalitis (TBE) virus and Lyme disease agents from males to females has been proved as well.

A cannibalistic type of pathogen exchange cannot be excluded as, for example, *Ixodes* tick males sometimes feed not only on fed females but also on hungry specimens.

At present, the classical pathway of pathogen transmission is no longer considered to be the main one. Pathogen exchanges between co-feeding vector specimens belonging to various age groups, for example, nymphs and larvae of ticks, or different generations, is now theoretically the most efficient way of spreading the viruses and other pathogens from infected individuals to uninfected ones. Ticks issuing saliva near each other may transfer regurgitated pathogens while feeding in the same site of inflammation in the host skin. This type of transmission is called transsalival and may occur both on viremic and aviremic vertebrate hosts (Fig. 16).



Pathogen Transmission by Arthropods, Figure 16 **Tick-borne encephalitis virus routes of transmission. I – "classical" (transmissive) route from egg to egg by feeding on the susceptible vertebrate animals with threshold quantity of virus in the blood; Ia – human infection by virus contained in goat or cow milk; II – transphasic transmission: naïve larva gets virus on infected susceptible vertebrate animal; III – sexual transmission: infected male transmits virus to naïve female during copulation; IV – virus exchange between infected nymphs and naïve larvae co-feeding not near each other on the vertebrate animal without viremia (distant transmission); V – virus exchange between specimens co-feeding near each other on aviremic (not susceptible to the virus) animal (transsalival transmission); VI cannibalistic route of transmission: infected male consumes hemolymph from naïve female and injects virus-infected saliva into her body; 1 – naïve tick and vertebrate animal: o – ova, L – larva, Lf – fed larva, N – nymph, Nf – fed nymph.**

Similar exchanges of pathogens, not only of viruses but of borreliae as well, occur when ticks feed separately on infected and aviremic animals. This type of transmission is termed infection on an aviremic host, or distant infection. The mechanism by which this exchange occurs is enabled by the host immune cells, which transfer absorbed pathogens from one area of inflammation to another.

The many forms of pathogen transmission ensure the effective transmission of infection by bloodsucking insects, mites and ticks.

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Pathogens of Whiteflies (Hemiptera: Aleyrodidae)

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Whiteflies are tropical and subtropical in origin, and can be serious pests in greenhouses and on house plants. In the United States, whiteflies were considered secondary pests in agricultural field crops until outbreaks of the silverleaf whitefly (*Bemisia argentifolii*) began to occur in the late 1980s. Before the development of the silverleaf whitefly problems in the U.S., whiteflies were mainly greenhouse pests, and occasionally pests on certain other subtropical crops, such as citrus. The silverleaf whitefly has a wide host range, including cotton, melon, soybean, and a variety of vegetable crops.

Whiteflies are very small insects, and like other Hemiptera, they have sucking mouthparts. Insect pathogens (also known as entomopathogens) in the groups bacteria, viruses, rickettsia, and protozoans nearly always infect hosts through the alimentary tract, and so the host must ingest the pathogen to become infected. Because whiteflies suck the phloem from plants, the only means by which they might ingest these pathogen groups is if they occur in the plant phloem. Entomopathogens have been known to occur and even grow within plants, but it is not very common, and for that reason, these pathogens are rare in whiteflies. This situation should not be confused with its reverse, that is, where the insect acts as a vector for plant pathogens, a much more common phenomenon. Whiteflies do act as vectors for plant pathogenic viruses, particularly the Gemini viruses.

Nearly all known whitefly pathogens are fungi, which can infect their hosts directly through the exoskeleton. Fungi in the phylum Deuteromycotina are the asexual fungi, and most all pathogens of whiteflies belong to this group. Conidia, asexually produced spores, are the infective units. These spores attach to the outside of the host, where they germinate, producing a germ tube. The germ tube will grow along the cuticle of the host until it finds a suitable site to penetrate and cause infection. The invasion process varies somewhat between species, but a good general description can be found by Hajak and St. Leger (1994).

Aschersonia spp. are fungal pathogens commonly found in whiteflies in the genus *Trialeuroides*. These fungi belong to the class Coelomycetes and are specific to whiteflies and coccids. Twenty-five species have been isolated from whiteflies. They produce conidia in structures called pycnidia. Different species of *Aschersonia* can be distinguished by the color of the conidia – usually reddish, orange, or yellow. *Aschersonia conidia* are coated in a hydrophilic mucus layer. This mucus is somewhat sticky and prevents them from readily being dispersed by wind, so *Aschersonia conidia* are usually dispersed by rainfall. Young whitefly nymphs are the most susceptible life stage, with the older nymphal stages being progressively less susceptible, and the adults resistant, to infection.

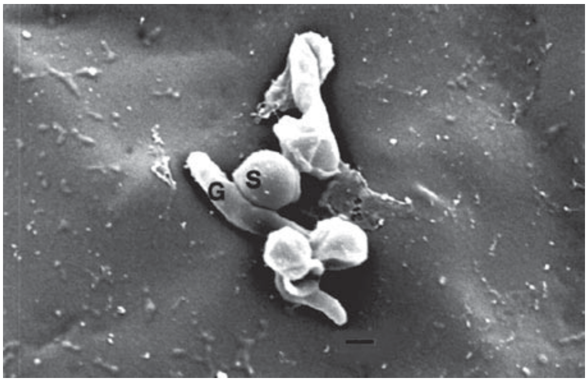
Other fungi that have been found in populations of *Trialeuroides* whitefly nymphs include *Verticillium lecanii*, *Paecilomyces fumosoroseus*, *Aphanocladium album*, and *Beauveria bassiana*. All these belong to the class Hyphomycetes. The nymphs are most commonly infected, but adults have been found infected with *Paecilomyces farinosis*, *Paecilomyces fumosoroseus*, *Verticillium fusisporum*, and *Erynia radicans*. Unlike the other fungi mentioned so far, *Paecilomyces* spp. and *Beauveria bassiana* produce dry conidia without a mucous coating. These may be dispersed by either rain or wind, but the spores are dried and shriveled and require high levels of moisture for germination. This moisture may come from rain, dew, or high levels of relative humidity that sometimes occur at the plant surface.

Aschersonia has rarely been isolated from *Bemisia* whitefly species. Pathogens in the genera *Verticillium* and *Paecilomyces* are much more common. *Beauveria bassiana* has been shown to infect nymphs of *Bemisia* whiteflies if they are sprayed with conidial suspensions, but no epizootics in untreated whitefly populations have been reported.

Pathogens of whiteflies have been used as biological control agents to control pest outbreaks. Using pathogens as biological control agents is also called microbial control, and is done two different ways: by natural epizootics and augmentative use. When whitefly populations reach outbreak levels and climatic conditions are right (usually during times of high rainfall), then fungal pathogens can cause epizootics. Epizootics of fungal pathogens in whiteflies can be quite striking and lead to a rapid decline in host populations. The limitation of natural epizootics as a pest control strategy is that growers have little control over their occurrence, and they often do not occur until host populations are high, which means that crop damage is likely to have already occurred. However, natural occurrences of fungal pathogens may control whitefly populations more often than is recognized.

Augmentative control is when a natural enemy is mass cultured and then released for biological control. The control agent may or may not be expected to establish in the region. It is the mass release that leads to control. This approach is common for microbial control agents; *Aschersonia*, *Verticillium lecanii*, *Paecilomyces fumosoroseus*, and *Beauveria bassiana* (Fig. 17) have all been produced for commercial sale as myco-pesticides against whiteflies. Most myco-pesticides used for whiteflies contain fungal spores, either conidia or blastospores, as the active ingredient. Conidia have a longer shelf- and field-life, but can only be produced on a solid substrate. Blastospores are produced during liquid fermentation. Liquid fermentation tends to be faster and less labor intensive than fermentation on a solid substrate.

These myco-pesticides have tended to work better in greenhouses than in field crops. The



Pathogens of Whiteflies (Hemiptera: Aleyrodidae), Figure 17 **Four conidia of the fungus *Beauveria bassiana* germinating on the cuticle of a nymph of the silverleaf whitefly. S = conidial spore, G = germ tube, Bar = 1 µm.**

reasons for this are surely many-fold, but the fact that greenhouses tend to be more controlled environments is probably a major factor. Temperature and relative humidity can have a dramatic impact on infection levels, and these factors are more controlled in greenhouses. The high levels of humidity in greenhouses are conducive to infection. Conidia and blastospores also are very sensitive to ultraviolet radiation, which is generally lower in a greenhouse than the field, just by the nature of a greenhouse (greenhouse materials such as glass, plastic, shade cloths, etc., block some light from entering). Lower ultraviolet light levels extend the life of the spores and their activity. In the field, mass immigration of new adult whiteflies into a treated field can lead to whitefly population increases if conditions are not conducive to disease transmission of the fungus from treated insects to new, uninfected hosts.

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Pathology

The science that deals with all aspects of disease.

Pathotype

An intraspecific variant of a pathogen, distinguished by variation in pathogenicity on a specific host relative to other pathogens of the same type.

Pathway

From a regulatory perspective, any means that allows the entry or spread of a pest into a new area.

Patrolling

In honey bees, the act of investigating the interior of the nest by workers. Such behavior allows the nest to detect and respond to problems quickly.

Patronym

In nomenclature, a scientific name of a taxon based upon the name of a person. When such a name is dedicated to a living person, it is said to be named for that person. When it is dedicated to a deceased person, it is said to be named after that person.

Paurometabolous Development

This is a type of incomplete metamorphosis (hemimetabolous development) found in some aquatic insects (Odonata, Ephemeroptera, Plecoptera). Unlike terrestrial insects displaying the typical form of incomplete metamorphosis, in which the immature and adult stages are substantially the same in body form (differing principally in the presence of fully formed wings among the adults), immature and adult stages of these aquatic insects differ slightly to significantly in appearance as compared to their adults. However, they lack a pupal stage, which is characteristic of insects with complete metamorphosis (holometabolous development). Because these insects depart from the typical pattern of hemimetabolous development, they sometimes are said to have paurometabolous development or gradual metamorphosis. Consistent with this differentiation, the immature are sometimes called naiads rather than nymphs. (contrast with hemimetabolous development, holometabolous development).

► Metamorphosis

Paykull, Gustaf

Gustaf Paykull was born at Stockholm, Sweden, on August 21, 1757. Educated initially by tutors, Paykull was likely influenced by Linnaeus, and developed interest in natural history, literature, and poetry. His literary successes were limited at the University of Uppsala, and he began to concentrate more on natural history. Beginning in 1779 he worked in government administration, though he found pleasure in collecting, and he also learned that this activity earned him respect from colleagues. He went on to build an extensive private collection of natural objects. He produced monographic treatments on several groups of beetles in the late 1700s, culminating in his "Insecta Svecica" (1798–1800). Paykull traveled widely, and collected birds, mammals, and fish in addition to insects. His eagerness to amass a large collection earned him the ire of some colleagues, however, as some borrowed specimens apparently were not returned. He was honored by election to the Swedish Academy of Sciences in 1791. Paykull died at Stockholm on January 28, 1826.

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Pban

A neuropeptide that controls synthesis of pheromone in glands of some female moths.

► Reproduction

PCR

See polymerase chain reaction.

PCR-RFLP

A technique that combines the PCR and RFLP analyses. Genomic DNA is amplified by traditional PCR. Once the DNA is amplified, it is cut with restriction enzymes, electrophoresed, and visualized by ethidium bromide staining. Because the DNA was amplified by the PCR, the DNA fragments can be visualized without having to blot and probe the labeled probe, making PCR-RFLP more efficient and inexpensive than traditional RFLP analysis.

Pea Aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae)

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The origin of pea aphid is likely Europe or Asia, although it is now found throughout the world in regions with temperate climates. In recent years, a closely related species with similar biology, *Acyrthosiphon kondoi* Shinji, has also spread nearly worldwide and attacks some of the same crops.

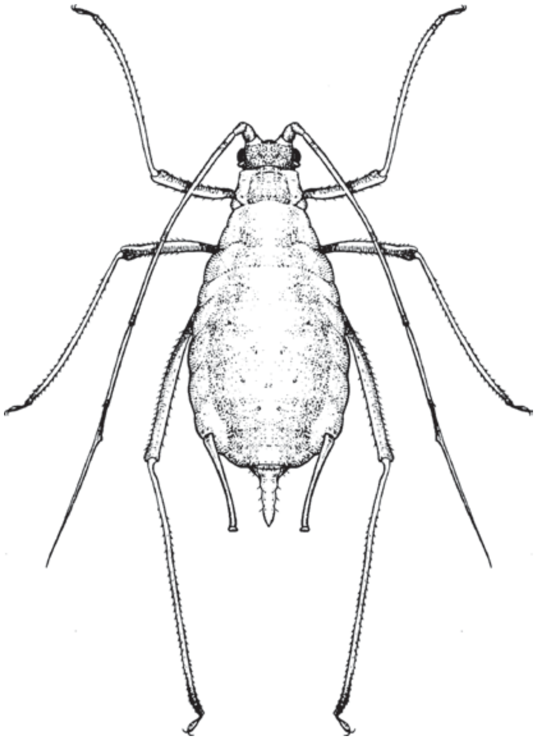
Life History

Pea aphids complete their life cycle quickly. These aphids can reach maturity and begin reproduction 10–12 days after birth. The number of generations completed annually by pea aphid is estimated at about 13 in cooler climates and over 20 in warmer climates. The overwintering stage of pea aphid varies with climate; in cold regions the eggs overwinter, in warm areas females persist, and in temperate climates both eggs and females can be found during winter months. Unlike many species of aphids, these species do not migrate to a woody host for overwintering. However, they do commonly disperse from annual legumes in the summer to perennial legumes such as alfalfa and clover in the autumn, so the difference in behavior is not great.

The egg is elliptical in shape, measuring about 0.75–0.80 mm long and 0.35–0.40 mm wide. Initially pale to bluish green in color, the eggs soon turn shiny black. Eggs commonly hatch in early spring. After developing on alfalfa or clover for several generations, overwintered populations produce winged females which disperse to uninfested plants. New hosts include both peas and forage legumes.

Pea aphid has four instars. Instar duration is about 2.7, 2.6, 2.7, and 3.6 days, respectively, at 15°C. Optimal temperatures are about 10–15°C for survival and fecundity, but 20–25°C for rapid development. Throughout development the nymphs are pale green in color. The body length increases from about 0.9, to 1.2, 1.7, and 2.0 mm in instars 1–4, respectively. The tip of the cornicles, distal portion of the tibia, and the tarsi are blackish throughout development. The instars are best separated by cornicle length, with lengths of <0.21, 0.21–0.36, 0.37–0.58, and >0.58 mm in instars 1–4, respectively.

Through most of the year, pea aphid reproduces parthenogenetically (viviparously), females giving birth without mating. Reproduction commences about 2.4 days after attainment of the adult stage. Reproducing females may be either winged (alate) or wingless (apterous) (Fig. 18). These are relatively large aphids, the apterae measuring about 2.3–2.7 mm and the alatae about 3.0–3.5 mm in length. Both winged and wingless forms are pale green with black at the tips of the rather long cornicles (Fig. 18), although in the alate form the head and thorax tend toward yellow-brown. Both forms also have long legs, principally green but with the tips of the tibia, and the entire tarsi, blackish in color. The wings of the alatae are colorless. Pea aphid sometimes exhibits red body color rather than green. The basis for the color forms is genetic, and in crosses the red form is dominant. Red color forms rarely are found on pea, but are sometimes found on red clover and alfalfa. Females typically begin production of offspring 10–12 days after birth. Mean number of nymphs produced per female is estimated at about 70–100, although some individuals produce up to 150 offspring. The rate of reproduction is highest early in life, with as many as 14 nymphs being produced per day by each female. Near the end of her life (mean of 40 days), an aphid may be producing less than one nymph per day. The average rate of reproduction is estimated at 7 per day, but apterous females produce 8.5 per day whereas alatae produce only 3.8 per day. The aphids seem to form only small colonies on pea, with frequent dispersal of alatae as densities increase. Maturation of pea plants also results in development of alatae, and their dispersal.



Pea Aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), Figure 18 Wingless adult female of pea aphid, *Acyrthosiphon pisum* (Harris).

Sexual forms are produced by pea aphid in the autumn in response to shorter day lengths and cooler temperatures, and males and females may be alate or apterous. The females greatly resemble the apterous viviparous females, differing principally in size. Oviparous females measure only about 2.0–2.2 mm long. The greenish males also bear brown coloration on the thorax, and usually brown or yellowish brown on the head and abdomen. The males measure less than 2.0 mm long. Production of sexual forms is less predictable than in many other species of aphids. For example, oviparous females may be produced by either alate or apterous females, and the same female may produce both viviparous and oviparous forms alternately. Fecundity of oviparous forms seems to be unknown, but based on examination of ovaries, at least 25 eggs are produced by each female.

The aphids produce and respond to alarm pheromone. Pheromone production normally results when aphids are disturbed, and the standard response by aphids is to walk away from the source of the pheromone or to drop from the plant. Responsiveness to pheromone is increased when the substrate is vibrated. Young instars are less responsive.

Pea aphids are known principally as pests of Leguminosae. Because they are efficient vectors of plant viruses, however, they also cause loss in crops on which they normally do not feed, such as cucurbits.

Pea aphid is prone to develop races or subspecies with slightly different host ranges, so populations may differ somewhat in their damage potential to specific legumes. Pea is the most suitable vegetable host for this species, and faba bean and lentil are sometimes damaged. Other hosts that are important in pea aphid biology are alfalfa, sweet pea, vetch, and such clovers as alsike clover, red clover, white clover, and sweet clover.

A large number of natural enemies of pea aphid have been documented. Flower fly (Diptera: Syrphidae) and ladybird larvae (Coleoptera: Coccinellidae) species are most numerous among the natural enemies, and sometimes quite important in regulating aphid population densities. However, fungi and wasps (Hymenoptera: principally Braconidae) also are very important, with introduced species of *Aphidius* normally dominant. The braconid *Aphidius ervi* Haliday is often reported to be the most important parasitoid, and was observed in North America soon after the introduction of pea aphid, probably being introduced simultaneously. Initially it did not provide effective suppression, and other introductions of beneficial species were made, apparently including additional subspecies or races of *A. ervi*. Among the other species introduced were *A. smithi* Sharma & Subba Rao; *A. eadyi* Stary, Gonzalez, & Hall; *A. urticae* Haliday; and *A. staryi* Chen, Gonzalez, & Luhman. Apparently there has been displacement among species and strains of parasitoids, with the native *A. pisivorus* Smith displaced by imported *A. smithi*, and then the latter species displaced by *A. ervi*.

A rather predictable cycle of events is observed in many pea aphid populations. After building to high densities on either forage legumes or peas in the spring months, predators, parasites, and fungi take a toll. Both the natural enemy densities and weather are unfavorable at mid-summer, and aphid populations decline. Warm, humid weather, in particular, favors development of fungal epizootics among pea aphids. With the subsequent collapse of natural enemy populations and the return of cooler, more favorable weather for aphids in the autumn, pea aphid populations typically increase again. In Canada and other northern latitudes the aphid populations may not attain high densities until late summer, so there is only one population peak.

In addition to the effect of weather on disease incidence, there also can be direct effects of weather on pea aphids. In cold climates, which are normally characterized by abundant snowfall, egg survival rates are high and overwintering success is not highly variable. In mild-winter areas, overwintering success is more variable. Mild winters favor the survival of overwintering females and eggs. During cold winters, however, when temperatures fall below freezing, neither adults nor eggs survive well. In addition to the cold temperatures, the lack of snow cover is thought to reduce the overwintering success rate. Also, aphids are especially susceptible to destruction by such adverse weather as heavy rainfall in the early part of the season, soon after egg hatch. The lower developmental threshold for pea aphid is about 5.5°C, whereas that of its principal parasitoids is 6–7°C. The higher developmental threshold of the parasitoids allows the aphid populations to increase to higher densities during cool spring weather.

Damage

Pea aphids cause direct injury by removal of plant sap from leaves, stems, blossoms, and pods. Aphids feeding on foliage disrupt the flow of plant photosynthates to the plant roots. Nitrogen fixing bacteria inhabiting the nodules on roots of legumes are affected by availability of phytosynthates. Thus, aphid feeding decreases nitrogen fixation and plant growth. Both young and mature plants are affected. Damage may not be apparent if aphid populations are low, but at high densities foliage may turn brown, pods are only partially filled, or fewer pods are produced. Under extreme conditions young plants are killed.

Pea plants may support aphids throughout the growing season, but not all stages of plant growth are equally susceptible to damage. The flowering and pod-filling stages were most susceptible to injury. Plants infested prior to the reproductive stage recover from damage if the aphids are removed, resulting in no reduction in yield. The treatment threshold was estimated to be about 2–3 aphids per stem tip, or 9–12 aphids per sweep.

Acyrthosiphon species commonly vector plant viruses. Over 30 viruses are known to be transmitted by pea aphid. Because pea aphid develop large populations on many legume hosts, particularly extensively planted forages such as alfalfa, they provide numerous potential vectors to cropping areas. In some instances they are important vectors in crops on which they do not normally feed. For example, watermelon mosaic virus and zucchini yellow mosaic virus are transmitted to cucurbits by both pea aphid and blue alfalfa aphid. They are very important in vectoring legume viruses also, including pea enation mosaic, one of the most prevalent virus diseases of peas.

Management

Aphids may be sampled by various methods, including direct visual examination of plants, sweeping, vacuum sampling, and trapping. Sweep net sampling is usually recommended.

Both soil-applied and foliar insecticides are commonly used to protect plants from injury by pea aphid. Systemic and nonsystemic products are used. The susceptibility of aphids to foliar insecticide is increased slightly when alarm pheromone is released near aphid-infested plants, presumably because the elevated activity level associated with pheromone release increases contact with insecticide.

Crop management is a key factor in preventing damage by pea aphid. Because alfalfa and clover are the common overwintering sites, they serve as the source of inoculum for surrounding areas. Such crops can be sprayed with insecticide or harvested before aphid populations produce alate forms, resulting in the destruction of most potential dispersants. Destruction of crop residue by burning also disrupts aphid populations by destroying overwintering aphids.

Forage legumes may serve as sources of plant viruses for both legume and nonlegume vegetable crops, and pea aphid serves as an effective vector. For example, the incidence of bean yellow mosaic virus in bean is related to the proximity of clover. Also, emigration of aphids from alfalfa to other crops increases following cutting.

Pea leaf roll, pea enation mosaic, and some other *Acyrthosiphon*-transmitted viruses are circulative viruses, persisting for the duration of the vector's life. Such viruses usually require extensive feeding for successful transmission; thus, insecticides can be helpful in protecting against disease. Research has shown that incidence of pea leaf roll virus can be decreased by application of systemic insecticides. Insecticides are less useful for stylet-borne viruses, which are transmitted quickly. Interestingly, stylet-borne virus transmission is often reduced by application of oils to plants, but oil does not greatly reduce transmission of circulative viruses such as pea enation virus. The differential effectiveness of oil is likely due to the tendency of oil to inhibit probing by transient alatae, but not feeding by colonizing aphids.

Peas differ in their susceptibility to pea aphid. Resistance is reflected in differences in aphid weight, longevity, time to maturity, and progeny and honeydew production on many plant cultivars, and in plant tolerance to aphids in a few varieties. Although aphid performance differs among pea cultivars, none are immune to attack. Faba bean cultivars, although differing with respect to aphid performance, similarly display little practical resistance to pea aphid. Pea plant morphology affects aphid success indirectly by influencing searching effectiveness of aphid predators, but this form of resistance has not been exploited by pea breeders.

► Aphids

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Peach Silver Mite, *Aculus cornutus* Banks (Acarina: Eriophyidae)

This mite damages peach tree foliage throughout the world.

► Four-Legged Mites

Peairs, Leonard Marion

Leonard Peairs was born at Leonard, Kansas, USA, on June 5, 1886. He obtained his B.S. and M.S. degrees from Kansas State University in 1905 and 1907, respectively. For several years he worked at the University of Illinois, University of Maryland, and Kansas State, but in 1912 he accepted employment at West Virginia University where he remained until retirement in 1952. In 1925 he received a doctorate from the University of Chicago. Peairs is best known as a co-author of the text "Insect pests of farm, garden, and orchard" (with E.D. Sanderson, 1921 and subsequent editions). He served as editor of the "Journal of Economic Entomology" from 1940 to 1953. Peairs died on January 29, 1956.

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Pea Leafminer, *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae)

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What is known today as the pea leafminer was originally described as five different fly species: *Agromyza huidobrensis* Blanchard (1926, Brazil), *Liriomyza huidobrensis* Blanchard (1938, Argentina), *L. cucumifoliae* Blanchard (1938, Argentina), *L. langei* Frick (1951, California), and *L. dianthi* Frick (1958, California). In 1973, Spencer synonymized the California and South American species under the name *Liriomyza huidobrensis*. Recent genetic evidence (in addition to observations of behavioral differences) strongly suggests that the species occurring in California and Hawaii is different from the South American species and that the name *L. langei* should be resurrected.

The pea leafminer is a small fly, less than 2.5 mm long, with a generally black body, and yellow face, frons and scutellum. Salient characteristics that distinguish *L. huidobrensis* from other members of the genus are as follows: the vertical bristles on the head are on a dark background contiguous with the black hind margin of the eye; the antennal segments are yellowish-brown and the distal third of the third segment is sometimes darkened; and the hind-corners of the mesonotum adjoining the scutellum are black. The posterior spiracles of the puparia have 6–9 pores.

Liriomyza huidobrensis was not considered a pest prior to the 1970s, when in South America, large amounts of insecticides were applied against the gelechid potato moth, *Scrobipalpula absoluta* (Meyrick). The leafminer became resistant to these insecticides and emerged as a secondary pest. In the late 1980s it spread from South America to Europe on cut flowers, quickly spread throughout Europe, and arrived in Israel in the early 1990s. The South American species also has spread to Kenya, South Africa and Indonesia.

The pea leafminer is truly polyphagous, feeding on a large number of flowers, vegetables and weeds. Some of the more important economic plants are Cucurbitaceae (gherkin, cucumber, melon), Leguminosae (numerous bean species), Solanaceae (pepper, tomato, potato, eggplant), Caryophyllaceae (*Dianthus* spp., *Gypsophilla* spp.), Chenopodiaceae (spinach, beet), Compositae (thistle, endive, aster, *Chrysanthemum* spp., *Gerbera* spp., lettuce), Cruciferae (Chinese cabbage, radish), Umbelliferae (carrot, celery, parsley), and Violaceae (*Viola* spp.).

Damage to plants occurs in two forms: aesthetic damage from feeding punctures and tunnels, and reduction of photosynthesis. Adult females puncture top and bottom surfaces of leaves with their ovipositor and feed on the plant juices. Adult males also feed at these same holes. The amount of stippling varies with plant species, varying from about 50 to 300 per day. Additionally, females lay eggs on the underside of leaves; larvae hatch and mine the leaves. Larval mines are typically along the midrib and lateral veins, although not exclusively so. Even in leaves with one larval mine, photosynthetic rates are significantly reduced because larval tunnels are in the spongy mesophyll where chloroplasts are located. The feeding punctures also significantly reduce photosynthetic rates and stomatal and mesophyll conductance.

Female flies live less than three weeks and males about a week. During her lifetime, a female lays an average of 8–14 eggs per day after a 1–2 day pre-ovipositional period. The egg stage lasts about 2–3 days depending on temperature and host plant. There are three instars in the leaf, and the mines become progressively larger with each molt. The duration of the larval stage depends on temperature and host plant, but averages about one week. The third instar chews a hole in the leaf surface and emerges completely from the leaf to pupate. There is a prepupal stage of 4–5 h duration between formation of the puparium and actual pupation. Pupae vary in color from a light brown to almost black, and live about one week.

Control measures for greenhouse and open field crops include biological, cultural/mechanical, chemical, and use of resistant plants. Biological control measures in greenhouses with releases of *Dacnusa sibirica* Telenga, *Opius pallipes* Wesmael and *Diglyphus isaea* Walker wasp parasitoids have been very successful on various crops. While natural parasitism in the field sometimes may be quite high, it is insufficient to control the leafminer. Release trials have shown that it is economically unfeasible to release sufficient parasitoids to achieve control in open field situations in celery. Some success has been achieved in applying entomopathogenic nematodes (*Steinernema feltiae* (Filipjev)) for control of the leafminer.

Cultural/mechanical control measures are relatively few in number. It is always important to maintain good agricultural practices – removing harvested plants from fields, maintaining control over weeds, etc. – to prevent the buildup of populations in these reservoirs. However, to date, trials with traps plants have been unsuccessful. Attempts have been made at mass trapping flies by circumscribing greenhouses with yellow sticky sheets or by dragging sheets of oil coated yellow plastic just above crops in open fields; these methods have reduced the numbers flies but have not significantly controlled the situation. Similarly, vacuum removal of flies has had limited success because they quickly reinvade the field. In South America, trials have been proceeding on developing cultivars of potatoes that are resistant to the leafminer by developing plants with a high density of glandular trichomes that interfere with feeding and oviposition.

Chemical control measures have had mixed results. The leafminer was discovered in Israel when conventional insecticides failed to control what were thought to be adult *L. trifolii*. Growers in Indonesia spray 2–3 times a week with a variety of 35 conventional insecticides in attempts to control the fly, with unsatisfactory results. On the other hand, efforts to control the larvae with translaminar insecticides (neem, cyromazine, abamectin, and spinosad) have been successful. Timing of insecticide application with these translaminar insecticides is critical and requires educating growers to treat the (unseen) larval population and not wait until large numbers of adults are observed, when insecticides essentially are useless.

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Pear Decline

This is a widespread disease of pear trees that is transmitted by pear psylla.

► Transmission of Plant Diseases by Insects
► Pear Psylla

Pear Psylla, *Cacopsylla pyricola* (Foerster) (Hemiptera: Psyllidae)

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At least seven species of pear-feeding psyllids in the genus *Cacopsylla* are recognized from Europe and North America, with unknown numbers of additional species occurring in Asia. Several of these species are pests of commercial pear (*Pyrus*), most notably *Cacopsylla pyricola* (Foerster) in North America and Europe, and *C. pyri* (L.) in Europe. The North American psyllid, *C. pyricola*, is not native to North America, but was introduced into the eastern United States in the early 1800s on infested pear seedlings imported from Europe. The pest rapidly dispersed from the eastern U.S., ultimately reaching the pear-growing regions of western North America in the early 1900s. The species apparently now occurs in all pear-growing regions of North America. With codling moth, *Cydia pomonella* (L.), pear psylla is the major insect pest attacking commercial pears in North America. It is estimated that 50–80% of the costs associated with controlling arthropod pests in pear orchards are directed at pear psylla and a few other soft-bodied arthropods.

The adult pear psylla (Fig. 19) is 2–2.5 mm in length, and in appearance resembles a miniature cicada. The insect is greenish to dark brown in color, depending upon time of year, as discussed below. Wings are held roof-like over the abdomen. Eggs are yellow and elongate, having a curled filament extending from one end. The eggs are inserted partially into the host plant, anchored by a small pedicel that appears to function at least partially in uptake of water from the host plant. Nymphs are yellow at hatch, becoming darker with successive molts. Late instar nymphs are flat and oval in shape, having large obvious wing pads. Nymphs of all ages have a pair of conspicuous red eyes at the front of the head (Fig. 19).

Pear Psylla, *Cacopsylla pyricola* (Foerster) (Hemiptera: Psyllidae), Figure 19 **Adult pear psylla.**

Pear psylla has a somewhat unusual life cycle. The species is seasonally dimorphic, producing a large, dark overwintering adult, or winterform, that is quite distinct from the smaller and light-colored summerform adult. The dimorphism is controlled by photoperiod; nymphs experiencing short-day condition develop into winterform adults, whereas those experiencing long-day conditions develop into summerform adults. The dimorphism is striking enough that the two morphotypes were once considered to be separate species. Pear psylla overwinters both in the pear orchard and outside of the orchard, often on other tree fruit species. Dispersal from the pear orchard in autumn by Pacific Northwest populations of psylla occurs in October and November, coinciding with leaf fall in pear. Reentry into the pear orchard by post-diapause winterforms begins in February. Pear psylla reallocates among orchards between fall and spring associated with this dispersal behavior.

Winterform adults overwinter in reproductive diapause, characterized by immature ovaries and a lack of mating. Diapause ends in mid-winter; in the Pacific Northwest, cold temperatures keep the insect quiescent until late winter. Egg-laying by post-diapause winterforms begins in late February or early March in Oregon and Washington growing regions. The first eggs are deposited directly in wood at the base of fruit and leaf buds. Oviposition then shifts to newly emerging foliage as it becomes available. Fecundity of the overwintered female is quite high, exceeding 1,000 eggs per female. There are five nymphal instars, requiring 3–4 weeks to complete development at moderate (20–25°C) temperatures. Offspring of the overwintered adults eventually eclose as summerform adults, in Washington growing regions first appearing in early May. Pear psylla has 2–4 summerform generations per year depending upon latitude. Fecundity of the summerform adult is lower than that of the winterform adult.

Pear psylla causes several types of damage in pear orchards: fruit russet, psylla shock, and pear decline. Of these, russet is of most concern to growers, and management protocols are generally aimed at preventing this injury. Fruit russet is caused by the feeding activities of nymphs. Immature pear psylla ingest large quantities of plant juices that are eliminated as honeydew during the digestive process. Nymph-produced honeydew is in the form of a syrupy liquid, and if the product is in contact with fruit for extended periods of time it causes dark blotches or streaks on the fruit surface. If the marking is highly noticeable, the fruit may be downgraded at harvest. The damage is exacerbated by a sooty mold fungus that colonizes honeydew.

Psylla shock is also caused by nymphs. At high densities, pear psylla causes tree stunting, premature leaf drop, reduced fruit size, and premature fruit drop, symptoms collectively termed psylla shock. Substantial losses in yield may accompany this damage, and the effects may actually carry-over from one year to the next, even in the absence of high psylla densities the second year.

Lastly, adult pear psylla vector a mycoplasma-like organism that is responsible for pear decline disease. The pathogen causes sieve-tube necrosis at the graft union, preventing tree-synthesized nutrients from reaching the roots. Symptoms of the disease include a slow to rapid decline in tree vigor, accompanied by reduced yield and often eventual death of the tree. Resistant rootstock has largely eliminated this problem from North American pear production.

Control recommendations for pear psylla generally emphasize destruction of the overwintered generation and offspring of the overwintered generation, as it is very difficult to control the summer generations. Successful control in early spring is necessary to prevent unmanageable problems during the growing season. Also, it is necessary to manage the spring generation because contamination of fruit by honeydew early in the growing season almost ensures that the fruit will be damaged by russet. A typical program for overwintered adults is characterized by the use of horticultural mineral oil, sulfur, and insecticide, the latter generally being a synthetic pyrethroid or chlorinated hydrocarbon. The initial applications occur in late winter when pear is still dormant, with additional applications repeated as necessary as the tree breaks dormancy. The initial spray should be delayed until re-entry by psylla into the orchard is mostly complete, but before significant levels of egg-laying has occurred. The oil applications cause delays in egg-laying by the returning winterform adults, resulting in increased synchronization of egg hatch in early spring. This increased synchrony simplifies subsequent pesticide-based control efforts. Summer control of pear psylla has become increasingly difficult because of resistance to insecticides. Currently, summer chemicals used include Mitac (amitraz), Agri-Mek (avermectin), and a neonicotinyl, Provado. Other products found to be useful against pear psylla include insect growth regulators, applied in spring, and kaolin particle film, used from late-winter through bloom. Kaolin is a wettable powder that dries to a white film on the tree and is an extremely effective feeding and oviposition deterrent to pear psylla. In some pear production areas of Washington State, the kaolin product Surround has substantially replaced the more traditional spring chemical controls.

Growers have certain horticultural practices that they use to simplify management. These practices include primarily strategies that make the tree less suitable or less attractive to psylla. For example, it is recommended that growers use only enough nitrogen fertilizer to produce good fruit set and fruit size, as excessive nitrogen leads to outbreaks of pear psylla. Similarly, pear trees should not be over-pruned, as this may prompt extensive growth of new foliage which is highly attractive to adults. Suckers and water sprouts should be removed from limbs, as these are a source of highly nutritious foliage.

The primary means of monitoring pear psylla for management decisions are by use of a beat tray (for sampling adults) and by taking leaf samples (for immature stages). The beat tray method involves holding a white, cloth-covered tray (generally 45 × 45 cm^2 in size) beneath a horizontal limb, and sharply jarring the limb with a piece of stiff rubber hose. Psylla that are dislodged onto the tray are then counted. Recommended sample sizes are 25 trays (trees) per 10–20 acre (about 4–8 ha) pear block. Samples should be taken at random locations throughout the block. For the immature stages, samples taken during the first generation should consist of fruit spurs, examined either with a hand lens or beneath a dissecting microscope. Recommended sample sizes are at least 10 spurs per block. Additional samples taken just after bloom may also be necessary. For these samples, one fully expanded leaf should be taken from each sampled spur, with 2 spurs taken per tree and 20 trees sampled per 20 acre pear block. Mid-season leaf samples for psylla eggs and nymphs should be taken from actively growing shoots, near the top of the tree if possible. Extension personnel recommend taking 50 leaves per block, comprising a mix of young and old leaves.

Treatment thresholds tend to be fairly inexact and assume that the type of damage to be prevented is fruit russet (having a lower threshold than that for psylla shock, the latter requiring high densities of nymphs). Thresholds for adult psylla are one or two per ten trays during late winter before the dormant spray, and one or two per tray during the spring and summer growing seasons. For the immature stages, treatment thresholds are 1–2 eggs or nymphs per fruit cluster in spring, and 0.25–0.5 nymphs per leaf during the summer sampling periods. It should be noted that susceptibility of fruit to russet damage depends upon a number of factors, including pear variety (naturally russetted varieties such as "Bosc" are less susceptible than clear-skinned varieties such as "Anjou"), fruit destination (russet is of little importance in fruit destined to be canned), and age of the fruit when marked. Thus, threshold decisions for psylla control depend upon factors other than just psylla density.

Lastly, natural enemies have the potential to play a large role in controlling pear psylla. Many scientists consider pear psylla to be an induced pest, in that insecticide use destroys natural enemies that would otherwise keep psylla in check. Pear psylla is attacked by a variety of specialist and generalist natural enemies. One of its most important enemies is a specialist parasitoid, *Trechnites insidiosus* (Crawford) (Hymenoptera: Encyrtidae), that may cause very high levels of parasitism in reduced-insecticide orchards. Predatory true bugs, including species of Anthocoridae (*Anthocoris* spp.) and Miridae (*Deraeocoris brevis* (Uhler), *Campylomma verbasci* (Meyer)) are very efficient predators of pear psylla and other soft-bodied pests in pear orchards. Ladybug beetles (Coleoptera: Coccinellidae), lacewing larvae (Neuroptera), and European earwig (*Forficula auricularia* L.) also prey on eggs and nymphs of pear psylla. The relative importance of the various taxa in controlling pear psylla remains unexplored, and merits study.

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Pebrine

A disease of the silkworm caused by the microsporidian *Nosema bombycis*.

Pecaroecidae

A family of sucking lice (order Phthiraptera). They sometimes are called peccary lice.

► Chewing and Sucking Lice

Peccary Lice

Members of the family Pecaroecidae (order Phthiraptera).

► Chewing and Sucking Lice

Peck, William Dandridge

William Peck was born at Boston, Massachusetts, USA, on May 8, 1763. He is sometimes known as America's first native entomologist, as those preceding him were immigrants from Europe. Peck graduated from Harvard University in 1782 and though he aspired to be a physician, he entered business, an occupation he found to be unsatisfactory. He and his father (a naval architect who also was discontented) moved to a small farm at Kittery, Maine, were he spent the next 20 years isolated but studying nature. He became an authority on plants, birds, fishes, and insects. In 1794 he published the first American paper on systematics, a description of four fishes. He began writing on insects in 1795 and won a prize from the Massachusetts Society for Promoting Agriculture for his publication on cankerworm in 1796. In 1805 he became a professor of Natural History

Peck, William Dandridge, Figure 20 **William Peck.**

at Harvard University and he went to Europe to study botanic gardens in preparation for establishment of a botanic garden at Harvard. There he became acquainted with important European naturalists including Linnaeus. He described a few species of insects, but unlike most naturalists and entomologists of the period, was more interested in the economic aspects of entomology. Peck (Fig. 20) taught a course on entomology while at Harvard, undoubtedly the first course of its kind in the United States. He published such articles as "The description and history of the cankerworm" (1795), "Natural history of the slugworm" (1799), and "Some notice of the insect which destroys the locust tree" (1819). He died at Cambridge, Massachusetts, on October 8, 1822.

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Pecten

Any series of bristles arranged like a comb. This term (or pecten teeth) is sometimes applied to rows of spines on the legs of pollen-gathering bees.

Pectinate

Having a series of slender projections from a slender shaft. Comb-like.

► Antennae of Hexapods

Pederin

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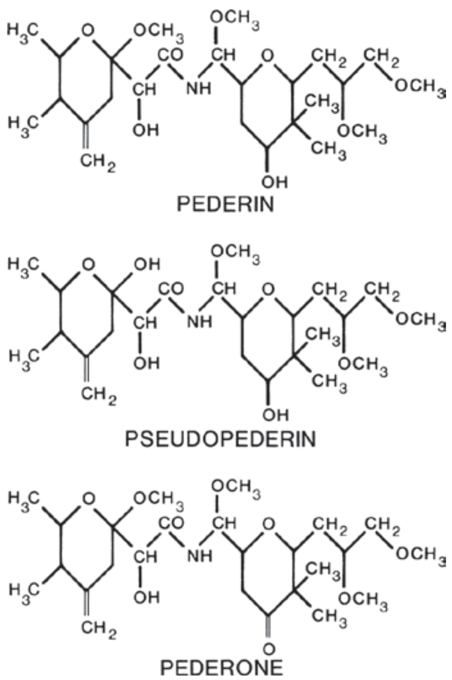
One of three toxins produced within some adult females of some species of *Paederus* and allied genera within the subtribe Paederina (Coleoptera: Staphylinidae: Paederinae). It is an amide with two tetrahydropyran rings, pederamide and pedaldehyde. The other two toxins are pseudopederin and pederone (Fig. 21).

Pederin is the most complex non-proteinaceous insect secretion known. It is among the most potent animal products known, more so than *Latrodectus* venom, which is 15 times more potent than cobra venom. It is a DNA-inhibitor and acts at the cellular level by blocking mitosis.

Pederin is produced within some females (those that contain certain endosymbiotic bacteria [+ females] and not within other females of the same species lacking endosymbiotic bacteria [-females, also called aposymbiotic females]) of some species of the staphylinid subtribe Paederina. It circulates in the hemolymph. It is accumulated in the eggs and thus is transferred to later stages (larvae, pupae, and resultant adults, male and female). Adult males and females are able to acquire pederin by cannibalism on their own immature stages. Those females in which bacteria



Pederin, Figure 21 **The structure of pederin, pseudopederin, and pederone. From Frank JH, Kanamitsu K (1987) *Paederus* sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. J Med Entomol 24:155–191, reproduced by permission of the Entomological Society of America.**

produce the toxin [+ females] typically contain much higher levels of it than do males (or females that do not produce it [- females]). The ability to produce it seems to be a matrilineal trait, because production does not seem heritable from males. The ability to produce it can be destroyed by use of certain antibiotics. Related toxins are produced in certain marine sponges.

Pederin is expressed from adult beetles when they are crushed. This occurs when adult beetles of some species fly to light (incandescent and fluorescent), inadvertently land on humans adjacent to the light, and are crushed (by human body parts) against the skin. The beetles do not attack people – instead, the harm is self-inflicted by humans. Typically, a hand is used to crush a beetle, and smears the exudate (pederin) in a line across the skin. Within 24-h a linear red mark of dermatitis is seen on the skin, thus the name "dermatitis linearis," or an injured eye swells and closes, causing temporary blindness.

It has been synthesized and, in pure form, it is a crystalline amide soluble in alcohol and water. It is more toxic externally and internally to rabbits, rats, mice, and guinea pigs than to hedgehogs, chickens, frogs, and toads. That suggests its purpose is not as a defensive secretion against vertebrate predators. It is not known to be toxic to insects, is not attractive to insects, and has little effect against bacteria. However, it has a demonstrated function in defense of the beetles against spiders, to which it is toxic. Other possible natural functions await exploration.

Experimentally, it has suppressed cancerous tumors in mice, rats, and plants, stimulated regeneration of damaged tissues, healed chronic necrotic lesions in geriatric patients, and induced cell fusion in human skin fibroblasts.

► *Paederus*
► Paederina
► Dermatitis Linearis
► Rove Beetles (Coleoptera: Staphylinidae)

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Pedicel

The constricted region of the abdomen in Hymenoptera. In ants the pedicel bears one or more upright lobes; the first segment is the petiole, the second the post-petiole. This term also is applied to the second segment of the antenna (Fig. 22).

► Antennae of Hexapods

Pedicinidae

A family of sucking lice (order Phthiraptera).

► Chewing and Sucking Lice

Pediculosis

The presence of lice on the body (= phthiriasis).

► Chewing and Sucking Lice (Phthiraptera)

► Human Lice

Pediculidae

A family of sucking lice (order Phthiraptera). They sometimes are called body lice.

► Chewing and Sucking Lice

► Human Lice

Pedipalps

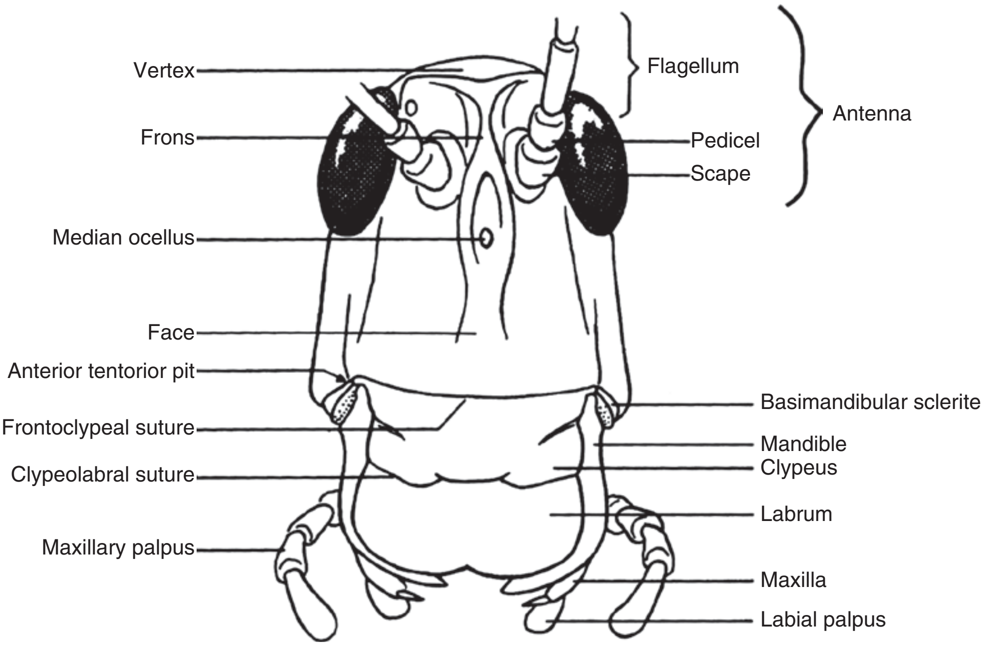
The second pair of appendages of an arachnid.

Pelagic Community

A group of organisms inhabiting the open sea, as opposed to the edge, or inlet of the sea or juncture of a river and an ocean (called estuarine).

Pedunculate

A structure positioned on a narrow stalk or stem-like structure (= petiolate).



Pedicel, Figure 22 **Front view of the head of an adult grasshopper, showing some major elements.**

Pelecinidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Pelecinid Wasps (Hymenoptera: Pelecinidae)

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Pelecinidae is a family of parasitic wasps with extant species found only in the New World. The family is contained within the superfamily Proctotrupoidea. This superfamily includes roughly 10–12 families, depending on the classification used, with the Diapriidae and Proctotrupidae containing the largest numbers of species. The others are considered to be relict families and contain few species. The Proctotrupoidea is probably paraphyletic. Most proctotrupoid families contain primarily small to minute wasps only a few millimeters in length, but the Pelecinidae is a notable exception, as described below.

Only one extant genus and three species of pelecinids are recognized: *Pelecinus thoracicus* Klug, *Pelecinus dichrous* Perty, and *Pelecinus polyturator* (Drury). *Pelecinus thoracicus* is found in western Mexico, and *P. dichrous* ranges across northern Argentina, Uruguay, Paraguay, and southeastern Brazil. *Pelecinus polyturator* has by far the largest latitudinal range, extending from southeastern Canada through the eastern and central United States and Mexico south to northern Argentina. Female *Pelecinus* are large (up to 7 cm in length), slender insects characterized by a very long, flexible metasoma (abdominal region), and swollen hind tibiae. Males are roughly half the length of females, with the posterior region of the metasoma swollen, giving the metasoma a club-shaped appearance. Both sexes have shortened basal tarsomeres of the hind legs. Body coloration of Nearctic specimens is almost always uniformly shiny black, with a white ring on each antenna. Specimens from tropical regions can be more variable, with red or reddish brown body coloration present. *Pelecinus* hold the wings elevated over the thorax at rest, rather than folding them flat over the back as most wasps do. The forewings are dark along the front edge, and this darkening may sometimes extend to some or even the entire wing. Wing venation is reduced in *Pelecinus*, which is an unusual feature for such large wasps. Reduced venation among wasps is generally confined to very small species.

Fossil Pelecinids

The fossil record has yielded several species of extinct pelecinids in the genera *Protopelecinus* and *Pelecinopteron*. Most of these have been found in Russia, Siberia, Mongolia, and the Baltic region. There is some disagreement regarding the status of several other controversial genera and species of fossil wasps uncovered primarily in China. These include members of the genera *Iscopinus*, *Sinopelecinus*, *Eopelecinus*, *Scorpiopelecinus*, and *Allopelecinus*, collectively referred to as "sinopelecines." Some consider these fossil wasps to be stem-group members of the Pelecinidae, and place them in the subfamily Iscopininae within the Pelecinidae. However, the prevailing view currently favors separation of these latter genera into their own family, the Iscopinidae, closely related to the Pelecinidae. Paleoentomological research on the pelecinids is very active, and hopefully future discoveries will clarify the evolutionary relationships among these groups. All of these fossil pelecinids and sinopelecines are small in body size (a centimeter or less in body length), in contrast to the much larger extant *Pelecinus*. Furthermore, a new fossil pelecinid species, representing a new genus, has recently been discovered in Cretaceous amber from New Jersey, USA. This "pygmy pelecinid," *Helopelecinus pygmaeus*, measures only about 6.5 mm in length, and represents the first pelecinid recorded in Cretaceous amber. All of the fossil pelecinids and sinopelecines have reduced wing venation, as is common among small parasitic wasps. This may explain why extant *Pelecinus* have reduced wing venation, even though they are quite large wasps. This condition may be an evolutionary holdover from smaller pelecinid ancestors. Effects of this evolutionarily constrained wing vein reduction on flight biomechanics of modern pelecinids is a potentially exciting area of research.

Ecology and Natural History

Despite their large size and striking appearance, relatively little is known of modern pelecinid ecology and natural history. Most published work has been on *P. polyturator* (Fig. 23). The vast majority of *P. polyturator* found in North America are females, as discussed below. Female *P. polyturator* are fairly common in the lower strata of hardwood forests, and are generally easily captured because of their slow flight. Once captured, the wasp may attempt to defend herself by stabbing with the metasoma, but has difficulty penetrating the skin. The relatively rare (at least in the northern part of their range) males are reportedly faster and more wary. *Pelecinus polyturator* are solitary endoparasitoids that primarily parasitize June beetle grubs of several species in the genus *Phyllophaga*, although *Podischnus agenor* has also been recorded as a host. Parasitism rates are reportedly very low, 1–3%, which suggests that *P. polyturator* is probably not an important factor in regulating host populations. *Pelecinus polyturator* host location behavior has been studied in a single hand-collected female kept in a terrarium with 6 cm of potting soil and 24 third-instar *Phyllophaga* grubs. The *P. polyturator* inserted her metasoma below the soil surface, probing both vertically and horizontally in the soil. She was able to reach grubs up to 5 cm below the soil surface. Several discrete insertions were observed, lasting from about one to almost seven minutes. Studies of larval *P. polyturator* dissected from *Phyllophaga* hosts have recorded lengths of 3.3–5.3 mm for first instars. The larvae were extracted from the posterior two-thirds of the host abdomen. They were dissected from hosts in the spring, which suggests that *P. polyturator* overwinter as late first instars within the host larva. The substantial size variation in adult *P. polyturator* may be associated with size variation in larvae of different host species.

Pelecinid Wasps (Hymenoptera: Pelecinidae), Figure 23 ***Pelecinus polyturator*** **(Drury) (Hymenoptera: Pelecinidae) is found throughout the Americas. (Photo by Lyle Buss.)**

Geographic Patterns

Pelecinus polyturator exhibits an interesting geographical pattern that was noted as early as 1928. In the southern, tropical part of its range, *P. polyturator* populations are bisexual and males are quite common. However, in the northern, temperate part of the range *P. polyturator* populations consist almost exclusively of females, which reproduce via parthenogenesis, development of an unfertilized egg into an adult. Males are very rare at northern latitudes, comprising at most 4% of the total population in Canada and the USA. This geographical pattern is known in a variety of animal groups, including some other insects, and has been given the name "geographic parthenogenesis." It has been suggested that this pattern occurs because parthenogenetic reproduction is evolutionarily favored over sexual reproduction in more marginal habitats (higher latitudes and altitudes, xeric vs. mesic habitats, disturbed vs. undisturbed habitats). These marginal habitats generally have lower populations, lower biodiversity, and fewer biotic interactions such as predation, parasitism, and competition. Thus, parthenogenetic populations should be more adaptive in these types of habitats because (i) finding a mate is unnecessary, which is advantageous at low population densities when finding a mate would be difficult, and (ii) fewer biotic interactions mean less selective pressure for the increased genetic diversity associated with sexual reproduction. It has been suggested that parthenogenetic populations of *P. polyturator* in Wisconsin may be associated with Pleistocene events, with all-female populations colonizing the recently unglaciated areas. It has also been suggested that the presence of *P. polyturator* males in a relatively small area in southeastern Wisconsin may represent the beginnings of displacement of a parthenogenetic population by a sexually reproducing population. Perhaps current climate change patterns could also have an impact on *Pelecinus* life history strategies.

The Pelecinidae represents a fascinating group of wasps and a rewarding subject of study. Continued research will undoubtedly provide further glimpses into the evolution, ecology, and biogeography of this enigmatic group.

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Pelecorhynchid Flies

Members of the family Pelecorhynchidae (order Diptera).

► Flies

Pelecorhynchidae

A family of flies (order Diptera). They commonly are known as pelecorhynchid flies.

► Flies

Peloridiidae

A family of bugs (order Hemiptera, suborder Coleorrhyncha). They also are known as moss bugs.

► Bugs

Peltoperlidae

A family of stoneflies (order Plecoptera). They sometimes are called roach stoneflies.

► Stoneflies

Pemphredonidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Penis (pl., penes)

The male intromittent organ. The aedeagus.

► Abdomen of Hexapods

Pentatomidae

A family of bugs (order Hemiptera). They sometimes are called stink bugs or shield bugs.

► Bugs

Penultimate

The next to the last. For example, the penultimate instar for a lepidopteran with six larval instars is the fifth instar.

Pepper Weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae)

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The pepper weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae), is a serious pest of peppers, *Capsicum* spp., causing millions of dollars damage annually in the southern U.S.A., Mexico, Central America, Hawaii and several Caribbean islands. Pepper weevil damages the pepper crop by directly feeding and ovipositing in the fruit, causing premature abscision of all stages of peppers from flower buds to maturing pods. This insect is generally more prevalent in warm climates and, based on the earliest records of this insect and the corresponding first records of a principal host plant group, the domesticated *Capsicum* spp. around 7000 B.C. in Mexico, it is probably native to Mexico or surrounding regions. The reason pepper weevil is such an important pest relates to the difficulty of controlling this insect once it has become established in the field. Larvae feed within pepper pods, and are protected from insecticide sprays. Also, since the level of weevils required to cause economic loss is so low, detection of this pest when it reaches an action threshold is time consuming and relatively difficult. The economic impact of pepper weevil as a pest of peppers in the U.S.A. is conservatively estimated at $5–$20 million annually and the impact of pepper weevil on Mexican pepper production is probably much greater. Current factors that keep potential losses due to pepper weevil from reaching 50–100% in more areas in the U.S. are the availability of effective insecticides and local eradications from harsh winters or the absence of host plants causing local extinctions.

The introduction of pepper weevil from Mexico into Texas is thought to have occurred through fresh market transport. In the USA, it occurs in Hawaii, California, Arizona, Texas, Louisiana, Florida, Georgia, North Carolina, and New Jersey. Outside the U.S. it occurs in Mexico, Guatemala, and El Salvador. Additional areas infested include Honduras, Puerto Rico, and Costa Rica. There is a report of pepper weevils in greenhouse production of pepper in Canada, apparently introduced on pepper transplants from southern California. This illustrates that pepper weevil can be introduced into any area that will sustain host plants for the pepper weevil and that re-infestations can even occur in areas where pepper weevil is periodically eradicated or does not normally exist because of climatic conditions.

The pepper weevil shares the same biological characteristics of many of the other 330 species of the genus *Anthonomus*. Adults are oligophagous, and females lay eggs in flower buds or fruit. Larvae complete development within immature buds or fruit, causing premature bud and fruit abscision (fruit drop). The pepper weevil has three larval instars and multiple generations per year. Reported generation times for the pepper weevil varies widely among different investigators from 10 to 40 days, with perhaps the largest differences occurring between summer and fall observations. Generation time, the number of generations per year (5–8), and longevity of adults (79–316 days) are determined primarily by host availability and temperature. The oviposition period ranges from 16 to 129 days and averages 30 days. Feeding and development of pepper weevil is limited to two host plant genera, *Capsicum* and *Solanum*, and limited in its northern distribution by temperature with the exception of introduction of infested plant material into northern greenhouses. The development time in pepper can be as short as 12 days, and in nightshade as short as 11 days.

Temperature data associated with development time were reported by several investigators. Emergence on artificial diet was observed in 17–18 days at 25.7–27.7°C and 70% relative humidity (RH). An average generation time of 17.5 days at 23.9–26.7°C and 60–85% RH. A mean generation time on bell pepper of 14.2 days at 25.7–27.7°C and 40–100% RH. Pepper weevil development has been related to growth stage and temperature by a regression of 1/days development (Y) to °C (X) for the period of adults to new emergence as

$$Y = -1.075 + 0.059X, R\hat{}^2 = 0.95$$

This data has been used to develop predictive models for pepper weevil population development in the field.

Several efforts have been made to define the relationship of crop damage to weevil infestation level. A pepper weevil population density exceeding 1 pepper weevil/100 terminal pepper buds can be economically damaging. Infestation levels of 5% damaged terminals, 1 pepper weevil/10 whole pepper plants, and 1 pepper weevil/400 terminal buds also were shown to result in significant economic loss in high-yielding bell peppers. The frequency of pepper weevil oviposition per fruit is a factor of time, pepper weevil population density, pepper fruit size and the plant variety. Varietal differences in peppers may affect host preference and these effects are thought to be negligible under heavy feeding and oviposition pressure. However, studies indicate that plant structure, number of fruiting buds per plant, etc., may affect the plant's ability to maintain greater numbers of unaffected mature pods.

Early attempts at scouting pepper weevil populations were simply presence determinations and, in many cases, the presence of fallen fruit was the first indication of a pepper weevil infestation. Examination of fallen buds for presence of pepper weevil immatures early in the season is a means of determining the presence of pepper weevil in the field. Counting fallen fruit or using a beat cloth are unacceptable sampling methods for timing pepper weevil control. However, inspecting terminal buds or bud clusters for pepper weevil adults was effective in predicting subsequent infestations. Yellow sticky trap captures correlate well with direct adult pepper weevil counts, using whole plant inspections, and the use of traps is an alternative to the more intensive and costly direct count method. It is also possible to monitor feeding or ovipositional damage to terminal bud clusters as a method for determining the presence of pepper weevil in commercial pepper fields.

The dispersion of pepper weevil has been investigated in several locations. The dispersion index developed for pepper weevil adults in Puerto Rico indicated that adult populations exhibited a moderately clumped dispersion in the field with a negative binomial k = 2.5. In Florida, weevils concentrate along field margins. Clumping patterns of pepper weevil have been confirmed in non-bell peppers. Early in the season, pepper weevil distribution is moderately to highly clumped and that there is generally a concentration of weevils along pepper field margins.

The majority of research literature on pepper weevil control is associated with chemical control. Natural enemies of the pepper weevil include various predators (e.g., *Solenopsis geminata*, *Strunella magna, Tetramorium guineese*) and parasites (e.g., *Pyometes venticosis*, *Catolaccus incertus*, *Pediculoides* *ventricosus*, *Bracon mellitor*, *Habrocytus piercei* and *Zatropis incertus*, *Catolaccus hunterii* and a new species of Braconidae, *Triaspis eugenii*). Classical biological control for pepper weevil was attempted with *Eupelmus cushmani* (Crawford) and *Catolaccus hunterii* Crawford in Hawaii, and with *Bracon vestiticida* (Vierick) in southern California with some establishment, but no documented success.

Movement to and from secondary host material and cull sites has been implicated as one of the primary causes for periodic re-infestation in commercial pepper fields. Also, because pepper weevil has been reported to reproduce on nightshade, *Solanum* spp., movement from nightshade to pepper is an important management consideration. Crop residue destruction, transplant sanitation, and nightshade management have been recommended as effective cultural controls of pepper weevil. Even so, caution should be taken with the timing of destruction of host material since the lack of oviposition sites may trigger the migration of weevils, as has been suggested with the boll weevil.

Considerable research needs to be conducted on pepper weevil. Pepper weevil pheromonal sex attraction and the use of yellow sticky traps are important in pepper weevil sampling and management. The males produce an airborne chemical that is attractant to the female, and males are not as attracted. More definitive information is needed on alternative management tactics, such as biological control, mating disruption with pheromones, natural mortality factors, and general ecology of pepper weevil, which ultimately will prove critical for managing this pest.

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Peradeniidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Perennial

A plant that lives at least 3 years and reproduces at least twice.

Pergidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Pericardial Cells

Loose clusters of cells that are found on or near the external surface of the heart. They are believed to have a phagocytic function, removing particulate matter from the hemolymph.

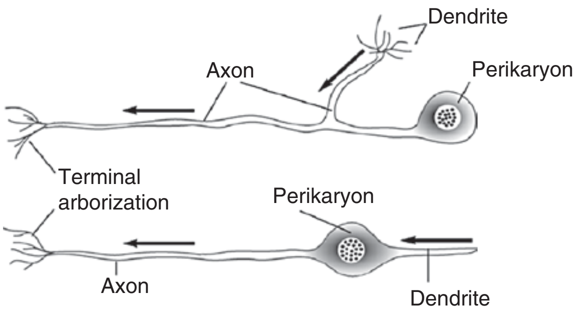
Pericardial Sinus

A space around the heart, bordered below by the dorsal diaphragm.

Perikaryon (pl., perikarya)

The cell body in a nerve cell. Also known as the soma (Fig. 24).

► Nervous System



Perikaryon (pl., perikarya), Figure 24 **Diagrams of insect nerve cells showing direction of nervous impulse (adapted from Chapman, The insects: structure and function)**

Perilampidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Perilestidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Periodical Cicadas, *Magicicada* spp. (Hemiptera: Cicadidae)

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Periodical cicadas (genus *Magicicada* Davis) are named for their extraordinarily regular adult appearances, caused by near-perfect synchronous development of the underground nymphs. Long life cycles of 13 or 17 years and large adult populations (up to about 3.75 million/ha, or 1.5 million/acre) make their periodicity events (Fig. 25) especially remarkable. Their importance has been long-standing, as can be seen in the following quote:

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 25 **Periodical cicadas emerge synchronously.**

"And the spring before, especially all the month of May, there was such a quantity of a great sort of flies like for bigness to wasps or bumblebees, which came out of holes in the ground and replenished all the woods, and ate the green things, and made such a constant yelling noise as made all the woods ring of them, and ready to deaf the hearers. They have not by the English been heard or seen before, or since." – William Bradford, second governor of Plymouth Colony, 1633

Up to four reproductively isolated *Magicicada* species commonly emerge together, apparently due to a dependence on predator satiation. *Magicicada* inhabit deciduous forests of the United States east of the Great Plains. Although locally synchronized, periodical cicadas in different regions mature and emerge in different years.

Although cicadas in other parts of the world sometimes damage crops such as asparagus and sugarcane, the periodical cicadas are not significant agricultural pests. Also, they are not harmful to humans or other animals.

The common name "periodical cicada" formally applies to *Magicicada septendecim* alone, but the plural form is widely applied to all members of the genus. No other strictly periodical cicada species are known. In the United States, the term "locust" is often incorrectly applied to cicadas (e.g., "17-year locust").

Morphology and Classification

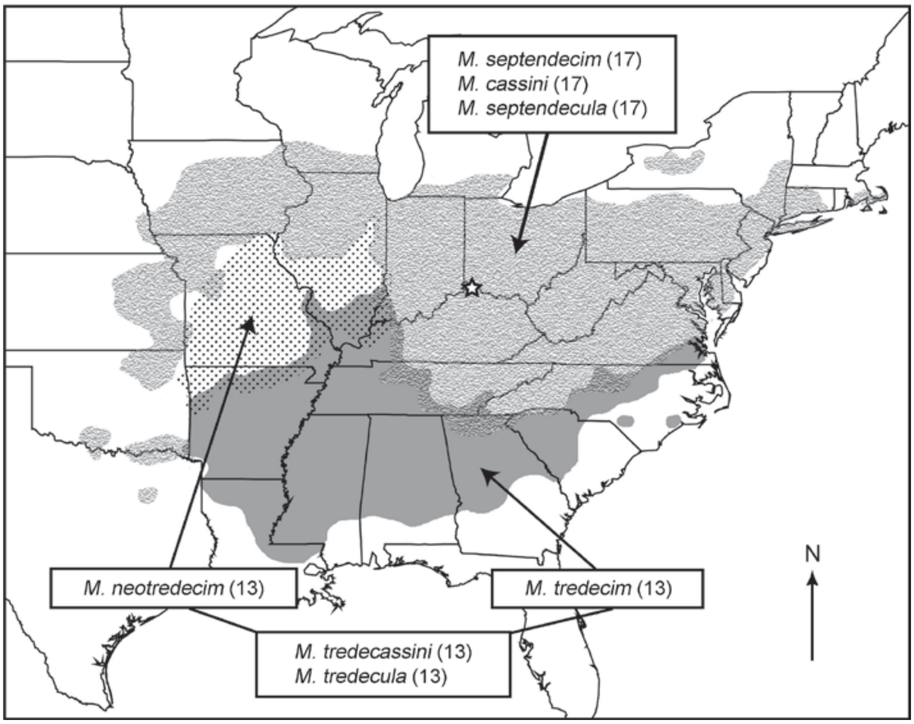
Periodical cicadas are medium-sized, about 2.5–4 cm from head to closed wingtip, with black-and-orange body coloration, striking red eyes, and orange-veined wings with distal infuscations. The seven *Magicicada* species (Fig. 26) are distinguishable by color pattern, song characters, and life cycle length. Three species groups are evident, the decim, cassini, and decula groups, and in each group one pair of species is distinguishable only by life cycle.

The relatives of *Magicicada* within the Cicadidae remain unknown. Morphological and genetic evidence supports their placement in the tribe Taphurini, subtribe Tryellina, but this largely Old World subtribe is represented in the Americas only by *Magicicada* and by a poorly known species recorded from Guatemala (*Chrysolasia guatemalena* (Distant, 1883)). Periodical cicadas are not related to the so-called "annual" cicadas of the genera *Okanagana* (which they resemble in appearance), *Tibicen*, and *Diceroprocta* that emerge throughout North America every summer.

Distribution

Species

The 17-year species are generally northern and range from Massachusetts to Iowa to Texas and



Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 26 Distributions of the seven *Magicicada* species. The star marks a newly reported, disjunct 13-year population.

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Table 7 Distinguishing characters of Magicicada species. Body length is the approximate distance from the tip of the head to the tip of the abdomen (holotype male, allotype female). Pronotal extension is the pronotal margin between the eye and wing articulation. Sternite color states are as follows: A, orange with dark centers; B, mostly orange; C, black, or with narrow orange bands less than one third of the sternite width; D, always with orange bands about one half of the sternite width. Phrase length is the duration of one song phrase. Song types are as follows: (i) pure tone, musical buzz ending in a drop in pitch (usually 2–3 song phrases between flights); (ii) rapid tick series then broad-spectrum buzz that rises and falls in pitch (usually 1–2 phrases between flights); (iii) repeated broad-spectrum chip-buzz phrases followed by chips without buzzes (usually one phrase between flights)

Species	Author (Year)	Life cycle	Body length (mm)	Pronotal extension color	Sternite color (each)	Dominant song pitch (kHz)	Phrase length (sec)	Song type
M. septendecim	Linnaeus (1758)	17	28,29	orange	A	1.25–1.5	1.5–4	1
M. neotredecim	Marshall and Cooley (2000)	13	28,29	orange	A	1.25–1.9	1.5–4	1
M. tredecim	Walsh and Riley (1868)	13	29,33	orange	B	1–1.25	1.5–4	1
M. cassini	Fisher (1851)	17	24,27	black	C	>3	2–4	2
M. tredecassini	Alexander and Moore (1962)	13	25,26	black	C	>3	2–4	2
M. septendecula	Alexander and Moore (1962)	17	24,26	black	D	>3	7–14	3
M. tredecula	Alexander and Moore (1962)	13	24,27	black	D	>3	7–14	3

northern Georgia (Fig. 26). All three are broadly sympatric (co-occurring) and synchronic (emerging together) (Fig. 27). The 13-year species, also synchronic, have more complex spatial relationships. *Magicicada tredecassini* and *M. tredecula* are sympatric from Maryland to Louisiana and north into Missouri and Illinois. The 13-year -decim species each inhabit part of the *M. tredecassini* + *M. tredecula* range and overlap one another along a zone extending from Arkansas to Indiana; in this zone, all four 13-year species emerge together. The northernmost *Magicicada* populations contain only *M. septendecim*, the most southwestern populations contain only *M. cassini*, and the -cassini species are locally rare or absent in the southeast. Periodical cicadas have been recorded from Ontario, Canada, but may now be extinct there.

Recent information suggests that an isolated 13-year population exists near Cincinnati, Ohio, surrounded by 17-year populations that have obscured its appearances historically. The next opportunity to confirm this population will arrive in 2014.

Broods

Same-cycle *Magicicada* populations in different regions have become temporally isolated by large-scale life cycle errors. The term *brood* is used for a set of such populations that emerge in the same year. There are twelve 17-year cicada broods and three

13-year broods (Table 8), most containing geographically contiguous populations. The broods have been named with Roman numerals reflecting their order of appearance, I-XVII for the 17 year broods and XVIII-XXX for the 13-year broods. Many brood numbers refer to years in the cycle for which no corresponding population is known. Some "empty" broods were recorded historically but have gone extinct, such as Brood XI in New England and Brood XXI in the Apalachicola River valley in Florida.

Most woods contain only one *Magicicada* brood, probably because resource levels are inadequate to support two populations large enough to satiate predators (see Predator satiation, below). As a result, the broods are mostly parapatric, meaning that their ranges overlap only along their edges. Some maps show extensive overlap between the 17-year broods XIV, X, VI, and II in the eastern states, and between the 13-year broods XIX and XXIII in the south. This may indicate that broods separated by four years or more experience reduced competition. However, some apparent overlap is explained by mistaken identification of straggling cicadas (see Life cycle plasticity, below) and imprecise county-level distribution records. Where two broods of different life cycles meet or overlap, local co-emergences occur every 13 × 17 or 221 years.

Predator Satiation

Many predators eat periodical cicadas when they emerge as adults, but the long periods between emergences prevent the predator populations from building up in response. Escape from ecological control by predators allows periodical cicada populations to reach extraordinary adult densities ranging from 8,000/ha–3.5 million/ha. Many cicadas and few predators means that the risk of being eaten is low for an individual cicada as long as it appears in synchrony with the brood. Furthermore, periodical cicadas have evolved in low-risk aggregations for so long that subsequent adaptations (e.g., precise but slow flight, low wariness, conspicuous mating behavior and bright coloration) have made them easy to catch and therefore dependent on large populations. Reproductive success increases with *Magicicada* population density, while adult mortality decreases. When periodical cicadas emerge in comparatively low numbers (roughly <5,000/ha), local predators easily drive the population extinct.

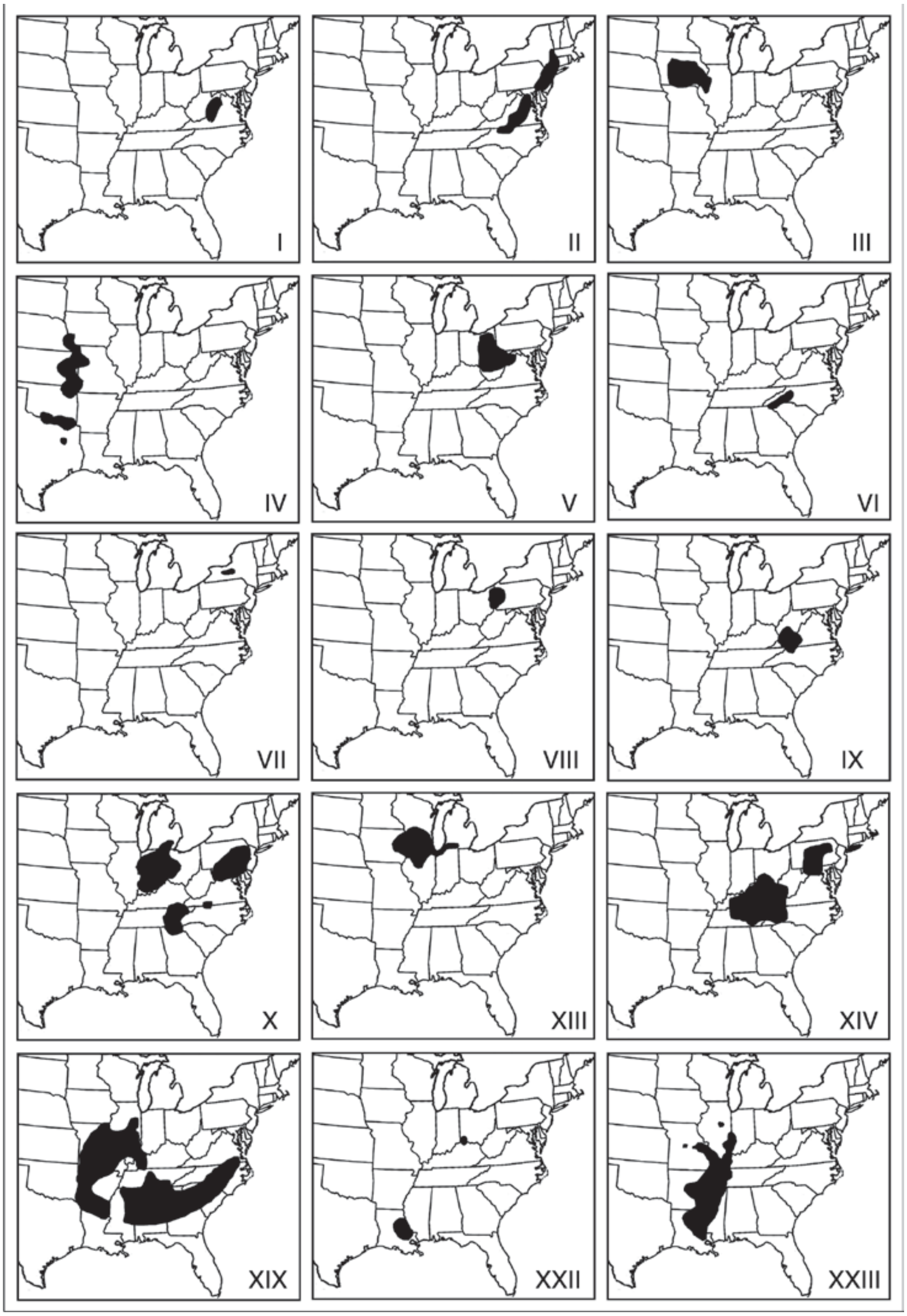
Juvenile Life History

Nymphal Development

Periodical cicadas begin life as eggs laid in pencil-sized twigs of trees or other woody vegetation. The eggs hatch six to ten weeks later, in midsummer, and the first-instar nymphs drop to the ground and seek feeding sites on small roots. Mortality approaches 98% during the first 2 years. All species pass through five instars and gradually move to larger roots. The durations of the first through fifth instars of 17-year cicadas have been estimated at 1, 2–3, 3, 5, and 5–6 years, respectively, with considerable variation across populations. Growth rates of 13-year nymphs differ from those of 17-year nymphs mainly in the first two instars. Nymphal growth rates also vary within populations; up to three instars can be observed at once although all eventually emerge together. Periodical cicadas, like all cicadas, suck fluids from plant xylem tissue, which is low in nutrients. Variation in growth rates within populations, together with considerable size variation among adults, suggest that competition for limited nutritive resources is important in dense *Magicicada* populations.

Life Cycle Timing

The mechanisms by which periodical cicadas "count" 13 or 17 years are unknown, but environmental cues are likely involved, such as temperature



Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 27 **Distributions of the fifteen extant periodical cicada broods.**

or other cues detected via their host plants. In one study, 15-year-old nymphs transferred to roots of greenhouse trees emerged in the 17th "greenhouse season," rather than their 17th year, when the seasonal cycle of the trees was artificially accelerated. Observations of off-schedule emergences also implicate external cues in developmental timing (see Life cycle plasticity, below).

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Table 8 **Recent and predicted emergences of the fifteen extant periodical cicada broods**

Year	17	13	Year	17	13	Year	17	13
1961	I		1984	VII		2007	XIII	
1962	II	XXII	1985	VIII	XIX	2008	XIV	
1963	III	XXIII	1986	IX		2009		
1964	IV		1987	X		2010		
1965	V		1988		XXII	2011		XIX
1966	VI		1989		XXIII	2012	I	
1967	VII		1990	XIII		2013	II	
1968	VIII		1991	XIV		2014	III	XXII
1969	IX		1992			2015	IV	XXIII
1970	X		1993			2016	V	
1971			1994			2017	VI	
1972		XIX	1995	I		2018	VII	
1973	XIII		1996	II		2019	VIII	
1974	XIV		1997	III		2020	IX	
1975		XXII	1998	IV	XIX	2021	X	
1976		XXIII	1999	V		2022		
1977			2000	VI		2023		
1978	I		2001	VII	XXII	2024	XIII	XIX
1979	II		2002	VIII	XXIII	2025	XIV	
1980	III		2003	IX		2026		
1981	IV		2004	X		2027		XXII
1982	V		2005			2028		XXIII
1983	VI		2006			2029	I	

Emergence and Teneral Period

In the spring, a few weeks prior to emergence, *Magicicada* nymphs construct emergence tunnels which they sometimes cap with mud "turrets" of unknown function. The nymphs wait below until the soil temperature reaches approximately 18°C at 20 cm depth. This threshold is reached in late April or early May in southern populations, and late May or early June in northern ones. Although temperature variation spreads the emergence over one to two weeks, a large fraction of the population may emerge on a single night, creating an extraordinary spectacle as thousands of ghostly-white teneral cicadas dangle from cast exoskeletons. The adult sex ratio is close to 50:50, but males emerge a few days earlier on average, a phenomenon called protandry. Emergence occurs after sunset, and ecdysis requires approximately one hour. Lack of perching space in dense emergences can cause a high rate of failed ecdysis.

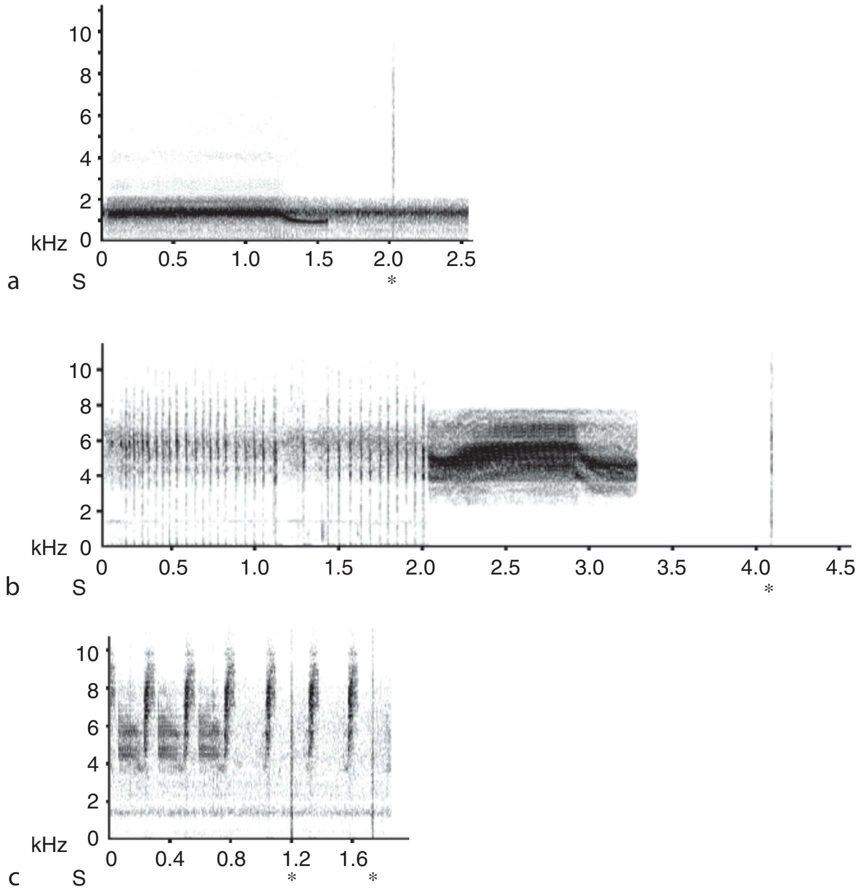
Complete hardening of the exoskeleton requires 5 days or more, depending on temperature, which explains the puzzling silence that immediately follows a large emergence. Once fully mature, males begin chorusing and females become sexually receptive. Individual adult cicadas survive approximately 2–4 weeks after emergence.

Adult Life History and Behavior

Chorusing and Mating

Males of all species fly to sunlit vegetation and alternate singing bouts of 1–3 song phrases with short flights. Both sexes are attracted to conspecific song, and periodical cicadas aggregate in chorusing centers that gradually move as the emergence progresses. These mating aggregations are viewed as non-resource-based leks, reflecting the absence of resources offered by males and the opportunity for female choice. Leks of different species frequently overlap, but the species are reproductively isolated by distinctive male songs and female phonoresponses (Fig. 28). Chorusing by the -decim species is most intense in the morning, -cassini activity peaks in the afternoon, and -decula peak at midday.

When ready to mate, females reply to conspecific males with wing-flicks after the male song phrase (in -decim and -cassini species) or after each of several cueing notes within the male song (-decula species). Males hearing or seeing wing-flick responses move toward the female and, in -decim and -cassini, switch to a courtship song of linked song phrases without gaps. Receptive females signal their continued willingness to mate



Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 28 Sonogram of one song phrase from the (A) -decim, (B) -cassini, and (C) -decula species group, including female wing-flick reply sound (marked with an asterisk) after species-specific delay. Only a central fragment of the long (7–12 sec) -decula phrase is shown. Note that the timescales are not equivalent, and that the -decim song phrase includes a strong acoustic background from other males.

by remaining still. Before copulation, the male switches to a second courtship song of staccato buzzes and makes initial contact with a vibrating foreleg. Acoustic courtship ends when copulation begins (Fig. 29). Mating lasts several hours and results in the deposition of a hardened copulatory plug in the female's genital tract. Most females mate once, although disruption of copulation can induce remating. Males can mate many times.

The synchronized emergence and the rarity of female remating lead to intense male competition for mates. Males listen and watch for female replies to the songs of competitor males as well as their own. While courting a female, a -decim or -cassini male will obscure the downslurs of nearby conspecifics with "interference buzzes" that prevent the female from hearing (and responding to) the potential competitors. High density and protandry of *Magicicada* choruses encourages lengthy courtships between mature males and still partially teneral, marginally receptive females. This, in turn, leads males to attempt mistaken courtships of conspecific males, other *Magicicada* individuals, and even inanimate objects.

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 29 **Mating pair of *Magicicada septendecim*.**

Under optimal conditions of light, warmth, and cicada density, males of the -cassini siblings exhibit synchronized chorusing behavior. In this "giant game of musical chairs," thousands of males together alternate synchronous song phrases with short flights, creating dramatic waves of song across the forest.

Oviposition

Mated females deposit eggs into twigs in forked rows using a sharp ovipositor, about twenty eggs per 1.5 cm egg clutch or "eggnest," and about 400–600 eggs per female. Eggnests from the three -decim species are wider and V-shaped, with ragged wood fibers. Those of the -cassini species are smaller and less ragged, and -decula eggnests have a braided appearance. Eggnest scars can be located and sometimes identified to species for many years. When oviposition space is scarce, damage from ovipositing females can cause breakage, or "flagging," of peripheral twigs. Perhaps because of the risk of flagging, female *Magicicada* avoid overlapping eggnests, even while demonstrating aggregative behavior at a larger spatial scale.

Ecology

The 17-year species have overlapping but distinguishable habitat preferences that are sometimes obscured in man-made environments. *Magicicada cassini* prefers deciduous lowland and floodplain woods, while *M. septendecim* and *M. septendecula* prefer deciduous upland woods, especially forest-prairie ecotones in the case of *M. septendecula*. Adult host plant affinities reflect these habitat preferences (e.g., *M. cassini* on elm and ash, and *M. septendecula* on hickory), although all species can use a variety of woody tree, shrub, and vine species. Host plant affinities of the 13- and 17-year siblings are indistinguishable. Adult periodical cicadas do not use soft plants such as grasses or forbs except as perches during ecdysis.

All *Magicicada* species avoid ovipositing in resinous conifers because sap seals the eggnests before hatching. Nymphs survive on roots of a wide variety of plants, including deciduous and coniferous trees.

Control Measures

Periodical cicadas require deciduous woods and do not affect most crops. They are not toxic or otherwise harmful to humans or other animals. Orchards, nurseries and gardens are sometimes affected when oviposition damages young trees and shrubs, and feeding by nymphs can reduce fruit yields. Adult xylem feeding does not cause noticeable damage. Some soil pesticides can kill cicada nymphs, but adult cicada populations are generally too large to be controlled by pesticides. Brood emergence schedules can be used to optimize the planting of young trees, and mesh covering (<1/2 cm gap) tied at the trunk protects saplings from females seeking oviposition sites.

Fungal Infection by *Massospora*

Periodical cicadas are tracked by one synchronized parasitoid, the entomopathogenic fungus *Massospora cicadina* Peck. The *Massospora* life cycle involves two stages that infect different cicadas in the same population. The first stage begins when nymphs are infected by diploid resting spores from the soil before emergence. During the first week after emergence, the fungus converts the contents of the abdomen into haploid conidiospores that will infect more cicadas from the same emergence. As the abdomen swells, the abdominal sclerites fall off and expose the chalky mass of spores. The fungus leaves the head and thorax intact and the cicada remains active, but both males and females infected with this stage become unnaturally sexually receptive. Infected males even wing-flick to other males, causing frequent male-male copulatory attempts. Infected females cannot complete normal mating and wing-flick to males until they die. Sexual contact may be important for conidiospore transfer.

Cicadas infected by conidiospores develop the second phase of the *Massospora* life cycle, a similar syndrome that eventually exposes a brown, fluffy mass of resting spores. These spores are dispersed over the soil by cicada movements, ready to infect the next generation of nymphs. No increased sexual receptivity is caused by the second *Massospora* stage, which does not gain from spreading spores to adult cicadas.

Life Cycle Plasticity and Speciation

Because each *Magicicada* species is most closely related to one with the alternative life cycle, periodical cicada speciation likely involves permanent life cycle shifts. Clues to the mechanism of speciation can be observed in the pattern of straggling, or off-schedule emergences of cicadas. Both premature and delayed straggling events have been recorded, with 1- and 4-year premature emergences especially common. Not surprisingly, geographically adjacent broods are often separated by 1 or 4 years. In addition, broods separated by 1 year are usually oriented north-south, with the earlier emerging brood found to the north. Brood formation occurs, then, when a rare environmental stimulus (e.g., climate shock) causes sufficient numbers of cicadas to emerge off-schedule and satiate predators.

For life cycle shifts to cause speciation, a permanent life cycle change must evolve, which implies an environmental cue that is maintained for generations. Such an evolutionary event has been proposed for *Magicicada neotredecim*. This 13-year species evolved recently from its 17-year relative *M. septendecim*, perhaps when sudden and extended mid-Holocene warming triggered a widespread four-year acceleration in development. Subsequent overlap and interaction between *M. neotredecim* and its 13-year relative, *M. tredecim*, led to reproductive character displacement in male song pitch and female song preferences.

Interspecific hybridization between the -decim, -cassini, and -decula groups can be encouraged in cages and leads to reproductively viable first-instar offspring, although adult hybrids have not been observed. Thirteen- and 17-year siblings apparently interbreed during their temporally and spatially limited co-emergences, although the genetic consequences of this for population divergence remain unknown.

Evolution of Periodicity

Many theories exist to explain the origin of life cycles that are extraordinarily long, developmentally synchronized, and prime-numbered. A popular "arms race" theory proposes that the *Magicicada* ancestor evolved a long life cycle to escape exploitation by a synchronized predator or parasite species, eventually settling on a prime-numbered solution that the parasitoid could not overlap with a shorter, common-factor cycle. This theory does not explain why just seven cicada species are periodical out of thousands worldwide.

Mathematical theories have shown that long, periodical cycles can arise from an interaction between demand for predator satiation and within-species competition for resources. But reliance on predator satiation is difficult to explain without pre-existing long, periodical life cycles. This illustrates the "chicken-and-egg" challenge presented by *Magicicada*.

More recent scenarios have focused on the climates that faced the *Magicicada* ancestor in eastern North America during the Pleistocene Epoch, when repeated glaciations spread cold, unstable conditions southward. Life cycles may have lengthened initially as a developmental side-effect of cold temperatures on nymphal metabolic rates. Alternatively, initial cycle lengthening may have occurred by natural selection because cicadas with longer cycles were less likely to emerge during unpredictable sets of cold years, when temperatures were too low for adult reproduction. Longer juvenile periods would increase cumulative juvenile mortality, creating selection for developmental synchrony (periodicity). Selection for developmental synchrony may have lengthened life cycles further if nutrient limitation prevents nymphs from emerging earlier. Finally, selection against hybridization between ancestral periodical populations with different life cycles (which would impede periodicity) might have favored those with rarely interacting prime-numbered lengths.

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Peripsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Periscelidid Flies

Members of the family Periscelididae (order Diptera).

► Flies

Periscelididae

A family of flies (order Diptera). They commonly are known as periscelidid flies.

► Flies

Perissommatidae

A family of flies (order Diptera).

► Flies

Peristome

In Diptera, the membranous area surrounding the base of the mouth.

Peritreme

Any sclerite bearing a body opening, particularly a spiracle. A sclerotic ring around a spiracle.

Peritrophic Membrane

A porous sheath lining the midgut and protecting the midgut cells from abrasion by the food, penetration by microbial pathogens, and the degradatory properties of digestive enzymes. It is secreted continuously along the length of the midgut (type I peritrophic membrane) or from the anterior portion of the midgut only (type II peritrophic membrane).

► Alimentary Canal and Digestion

Perlidae

A family of stoneflies (order Plecoptera). They sometimes are called common stoneflies.

► Stoneflies

Perlodidae

A family of stoneflies (order Plecoptera).

► Stoneflies

Peroral

By way of or through the mouth; *per os*.

per os

By way of the mouth; peroral.

Persistent Virus

A virus that passes through the body of the vector, and that usually persists for the remainder of the vector's life.

Pest Free Area

From a regulatory perspective, this is an area in which a pest does not occur, as demonstrated by scientific evidence, and in which this condition is being officially maintained.

► Pest Risk Analysis (Assessment)

Pesticide

A material that kills pests. This term is often used to describe insecticides, which are pesticides that kill insects.

Pesticide Hormoligosis

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Hormoligosis (from the Greek: *hormo* = excite and *oligo* = small quantities) is a term applied to the phenomenon in which sublethal quantities of stress agents such as chemicals, antibiotics, hormones, temperature, radiation, and minor wounds are stimulatory to an organism by providing increased efficiency to develop new or better systems to cope in a suboptimum environment.

The occurrence of pesticide hormoligosis in agriculture is well documented and may be a common phenomenon, but it is rarely monitored so we are uncertain of its importance in fostering outbreaks of certain pests or in accounting for failures in pest control programs. The purpose of this section is, therefore, to review the state-of-the-art of pesticide hormoligosis and to discuss controversial hypotheses on the reasons for the resurgence of certain arthropod pests and the drastic increase in their populations. Medical studies show that (i) stimulation of tissue repair after a sublethal dose of CCl_4 (i.e., chemically induced hepatotoxicity) appears to be the central mechanism in protection against death from a subsequent large dose; (ii) sublethal environmental stresses by exposure to ethanol (5%, v/v), acid (HCl, pH 4.5–5.0), H_2O_2 (500 ppm) or NaCl (7%, w/v), protects *Listeria monocytogenes* against lethal preservation factors by increasing its resistance to lethal doses of the corresponding factors; and (iii) pre-exposure of *Vibrio cholerae* cells to sublethal dose of 1.7 Gy X-rays makes these cells 3–38-fold more resistant to the subsequent challenge by X-rays.

In spite of a good initial kill at the time of treatment, different pesticides and even carrier materials and diluents used on orchard or field crops are reported to cause a tremendous increase of the pest against which they have been applied. Furthermore, spray applications are sometimes followed by serious outbreaks, not of the pest against which they were applied, but of other phytophagous insects and mites which, prior to the treatment, were in very small numbers too low to be of economic importance. Both types of increases, usually called pest resurgence, have been recorded in different climatic conditions (namely, temperate, subtropical and tropical regions) and for many species of the following families of mites or insects: Tetranychidae, Eriophyidae, Tarsonemidae, Coccidae, Aphidae, Aleyrodidae, Cicadellidae, Noctuidae, Tortricidae (=Olethreutidae), Yponomeutidae, Trypetidae, Agromyzidae, and the order Collembola. Spread of this phenomenon over a number of very different groups of phytophagous arthropods, and its occurrence after application of pesticides using different modes of action and under different climatic conditions, indicates that chemical control in these cases upsets the population dynamics of the pests in question.

For an explanation of this phenomenon, three hypotheses usually are suggested: (i) The reduction of natural enemies by the pesticides; (ii) pesticide-induced reproductive stimulation of phytophagous arthropods; and (iii) the removal of competitive species. Two additional factors also have been proposed: (i) altered host plant quality caused by agrochemicals, and (ii) the pesticide-induced irritation causing pest dispersal. Although sporadic literature confirms the validity of the second hypothesis (i.e., pesticide-induced reproductive stimulation of phytophagous arthropods), and its importance in pest resurgences, most information on the subject refers chiefly to the destructive effects of pesticides on the natural enemies of the phytophagous species and, to a lesser extent, to the removal of competitive fauna. Critical information needed to substantiate the importance of natural enemies in regulating pest populations includes: (a) a negative correlation between the number of natural enemies and pests, (b) proof that the natural enemies were the limiting factor to the density of the population, and (c) an exclusion of stimulating influences of the pesticide on the pest directly or via the plant. The less well-known phenomenon, pesticide-induced reproductive stimulation of phytophagous arthropods, comprises the backbone of pesticide hormoligosis and is the focus here.

There is considerable evidence of a favorable effect of some pesticides on the biotic potential of arthropods. For example, a drastic increase in the population of the fruit tree red spider mite, *Metatetranychus ulmi* (Koch) [*Panonychus ulmi* Koch], following the application of DDT has been demonstrated in The Netherlands since the late 1940s. Studies on the sublethal effect of DDT on oviposition of this mite revealed stimulation of egg production at a DDT concentration much lower than the recommended rates (Table 9).

In California, the results of a 3-year field and greenhouse study with DDT on natural populations and fecundity tests in small cages on the European red mite, *Paratetranychus pilosus* C. & F., failed to support the theory of destruction of the natural enemies as the primary cause of the mite outbreaks. Some of the results were, however, consistent with the idea of a physiological stimulus to reproduction under DDT influence.

Pesticide Hormoligosis, Table 9 Oviposition of *Panonychus ulmi* Koch on leaf discs treated with different concentrations of DDT dust during a 8–10-day observation

Treatment	Total eggs produced by ten females[a]	Egg production (index)
Control	37	100.0
1/8	78	210.8
1/4	24	64.9
1/2	31	83.8
1	23	62.2

[a] Average of five replicates(1 = field application rate amounting to 2.5 g/m^2 of dust containing 5% DDT; See Hueck DJ, Huenen DJ, Den Boer PJ, Jaeger-Draafsel E (1950) The increase of egg production of the fruit tree red spider mite (*Metatetranychus ulmi* Koch) under influence DDT. Physiol comp oecol 2:371–375, for more details)

Although some scientists at first thought that the mite resurgence was solely attributable to an elimination of the natural enemies of the mites, others posed the question of the possible involvement of a change in the physiology of the mites, or in their host, or both. It was found that DDT treatments produced an increase of mite populations above that occurring on check trees which was not explainable by a reduction of the natural enemies.

In order to find the reason for the mite's resurgence, apple trees with a moderate infestation of red spider mites were sprayed with parathion which killed all mites that were not in the egg stage, and all predators. Following the application of parathion, a number of trees were sprayed with DDT. Afterward, the numbers of all stages of red spider mites were counted every second day. An examination of the resulting data showed that egg production had been substantially higher on DDT-sprayed trees than on the check trees. Laboratory experiments also showed that the egg production of the mites feeding on leaf discs dusted with 5% DDT was significantly greater than those feeding on untreated discs. Both experiments, however, were not designed to explore whether the stimulating factor was caused by a direct influence of the pesticide, or via the plant. Coding moth adults, exposed to various sublethal doses of several insecticides, demonstrated stimulation of oviposition at concentrations where the females are under stress. Wherever the stress factors are not remarkable, oviposition is not stimulated.

More recent studies on population changes of spider mites (Acari: Tetranychidae) following insecticide applications in corn have shown that the exposure of twospotted spider mite (*Tetranychus urticae* Koch) to sublethal doses of permethrin leads to an increase in dispersal behavior (under laboratory conditions) and to an increase in population densities (under field conditions).

Stimulation of some vegetable plants by DDT with an action resembling that of some plant hormones suggests direct or indirect effect of sublethal doses of pesticides on phytophagous pests, but no field experiments or laboratory/greenhouse tests have been conducted either on intact or on excised plants (i.e., leaf discs). Nevertheless, numerous scientists have suggested the host-plant physiology hypothesis for the observed data on the reproductive stimulation of mites/insects whenever the hypothesis on the reduction in natural enemies is refuted. This hypothesis warrants additional research.

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Pesticide Resistance Management

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“Integrated Pest Management” (IPM) and “Management of Pesticide Resistance in pest arthropods” (MPR) are usually perceived to be distinct topics, but have equivalent goals and methods. Effective management of resistance to pesticides and effective IPM programs require that we employ a holistic and multitactic management strategy. A key component of a holistic and multitactic strategy will include enhancing the compatibility of pesticides and biological control agents.

Resistance to pesticides is an extremely important problem. At least 440 arthropod species have become resistant to insecticides and acaricides, with many species having become resistant to all the major classes of such products. Resistance to pesticides in weeds, plant pathogens, and nematodes also is increasing, although somewhat more slowly.

Developing and registering new pesticides is an elaborate, and increasingly expensive, business in most parts of the world. Thus, pesticide producers should be increasingly interested in extending the economic life of their products in order to maximize a return on their investment. Likewise, pest management specialists want to preserve registered pesticides. This is especially true for products that are effective against arthropod pests in minor crops such as vegetables, which may be ignored by pesticide companies because they are a relatively small market compared to field crops. Registration of new pesticides is likely to be more difficult and expensive in the future, which could leave some pest management specialists with extremely limited options for managing certain recalcitrant pests.

A few environmentalists have argued that we do not need pesticides, that they will soon be outlawed, or that they will become unimportant because transgenic crops resistant to pests and diseases will dominate the market, and that pesticide resistance will no longer be an important issue. However, it is unrealistic to eliminate all pesticides from agriculture; there are significant arthropod pests for which we have no other effective control tactic. Pesticides are effective tools for fighting outbreaks and emergency pest problems. Pesticides are often required to control plant pathogens, weeds, or nematodes because they cannot be controlled by alternative methods at this time.

Research on Resistance in Arthropods

Scientists have approached the problem of pesticide resistance in a variety of ways. Fundamental research over the past 40 years has produced insights into resistance mechanisms and the mode of inheritance of resistance in arthropods. Simulation models have been developed to evaluate different options for managing resistance, but these models may not be applicable to a specific situation.

The debate over whether to recommend alternation of different pesticides or to recommend mixtures of different pesticides as appropriate methods for slowing the development of resistance remains controversial. Each management approach is dependent upon specific genetic and operational assumptions associated with the resistance mechanisms and mode of inheritance of the resistance in the specific pest population, as well as application methods and timing, and details of the biology of the pest. If one or more of these assumptions are not valid, then the management recommendations may not result in the intended preservation of the pesticide. Furthermore, few field data are available to support adopting either alternation or mixtures, or other resistance management concepts.

The hypothesis that reduced fitness, which is often associated with pesticide resistance alleles, could be used in resistance management programs continues to be controversial. The concept of reduced fitness may have limited application because not all resistance alleles confer lowered fitness and selection for modifying genes that restore fitness to individuals carrying resistance alleles can occur in the field.

Various monitoring techniques have been developed to identify resistant insects or mites and detect their establishment and spread. These monitoring methods are particularly useful for documenting that resistance has developed, but monitoring methods that would allow us to detect rare resistant individuals in populations in sufficient time that operational pest management programs could be altered remains difficult and expensive to execute.

Resistance management research programs and IPM research programs have had fairly distinct identities to date. The current scenario usually goes something like this: Once a pesticide has been registered and used, and resistant individuals have been detected in populations, people begin to discuss developing and implementing a resistance management program. This approach is short sighted because an effective program is exceedingly difficult to execute in sufficient time to have the desired results.

Developing a resistance management program may take several years; studies typically are conducted to develop an appropriate monitoring method, estimate the frequency of resistant individuals in populations, detect cross resistances, and evaluate mode of inheritance and stability of the resistance. Meanwhile, unless pesticide applications are discontinued, selection for resistance continues. Because the initial detection of resistance usually requires that resistant individuals comprise 5% of the population, by the time resistant individuals are detected additional pesticide applications are likely to increase significantly their frequency in the population. This scenario is particularly familiar with pests such as aphids, spider mites, whiteflies, and leafminers with a high reproductive rate and multiple generations a year.

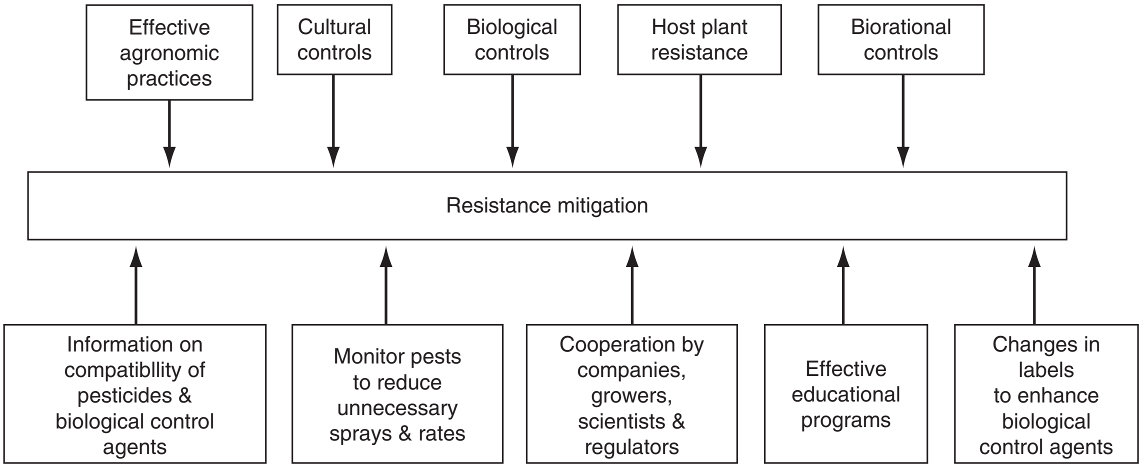
The experiences of scientists studying pesticide resistance in ubiquitous pests in other geographic regions can alert pest managers to a potential problem, but this seems to be an inefficient method for managing resistance in arthropods and it is possible for two different populations of the same species to respond to selection for resistance in different ways because different resistance alleles may be present in the different populations. Mechanisms may vary, the mode of inheritance may vary, and the degree of reduction in fitness associated with the resistance may vary because resistance alleles at each site are different. Because it is difficult to sample rare individuals in natural populations, monitoring programs, if employed other than as a method to document a problem once it has developed, may not be cost effective. Waiting until the pest becomes resistant before instituting a resistance management program is ineffective.

Resistance Management and IPM

A better paradigm for managing resistance in arthropods involves altering pesticide use patterns. Nearly everyone will agree that reducing pesticide use is an effective resistance management tactic. What is more controversial is whether resistance management programs should include altering the way pesticides are developed and registered. Also, many pest managers have been slow to recognize that resistance management must be a broad-based, multitactic endeavor (Fig. 30).

It seems reasonable to assume that nearly all major insect and mite pests will develop resistances to all classes of pesticides given sufficient selection pressure over sufficient time. There may be some exceptions, but this generalization appears reasonable given the documented record of resistance development in arthropod pests during the past 40 years. Resistance to stress is a fundamental and natural response by living organisms. On an evolutionary time scale we should expect insects to have developed multiple and diverse mechanisms to survive extreme temperatures, allelochemicals, and other environmental stresses. We should expect most insects and mites to develop resistance to most pesticides if subjected to appropriate and sustained selection. While new pesticide classes have been proclaimed to be a potential "silver bullet" and not amenable to resistance development, these hopes have been misplaced repeatedly. It seems appropriate to assume that the development of resistance is nearly inevitable and the issue is not whether resistance will develop, but when. With this assumption, resistance management programs have the goal of delaying, rather than preventing, resistance.

Growers and pest management experts cannot afford to rely on pesticides as their primary management tool. There are increasing social, economic, and ecological pressures to reduce pesticide use and to increase the use of nonchemical control tactics such as host plant resistance, cultural controls, biological controls and biorational control methods such as mass trapping, sterile insect release programs and mating disruption. There is an increasing emphasis to use pesticides that are nontoxic to biological control agents, and that have minimal impacts on the environment and on human health. The compatibility of pesticides with natural enemies and other nonchemical management tactics is critical for improving pest management programs and environmental quality,



Pesticide Resistance Management, Figure 30 Effective resistance management programs incorporate multiple tactics as part of a fully integrated pest management program. Pesticides should be used only when needed, at the lowest rates possible, and in a manner that reduces negative effects on arthropod natural enemies. Ideally, pesticide labels would include information about their effects on natural enemies.

as well as for managing resistance to pesticides in pest arthropods. Enhancing the compatibility of pesticides and biological control agents is complex and sometimes difficult, but can play handsome dividends in improved pest control and pesticide resistance management.

Changing the way pesticides are registered could become part of an effective resistance management strategy and would have the benefit of achieving improved integrated pest management. For example, some pesticides are relatively nontoxic to important natural enemies in cropping systems when applied at low rates, but the recommended application rates are too high. Use at the high rates thus disrupts effective natural enemies, leading to additional pesticide applications, which exert unnecessary selection for resistance in the pest. Under these circumstances, it may be appropriate for the label to contain two different directions for use; one rate could be recommended for the strategy of relying on pesticides to provide control. A lower rate could be recommended for use in an IPM program when it is known that effective natural enemies are present but need help to suppress the pest population(s). This approach to labeling could reduce the number of pesticide applications and reduce rates, which would reduce selection for resistance in both target and nontarget pests in the cropping system.

Another innovation in pesticide registration would require that the toxicity of the pesticide to a selected list of biological control agents be determined for each cropping system. This information should be provided, either on the label or in readily available computerized data bases, perhaps via the internet. Without such information, pesticides may be used that disrupt effective natural enemies. This often results in unnecessary use of pesticides, leading to more rapid evolution of pesticide resistance in pests. Enhancing biological control not only can lead to improved pest management, but is an essential tool in managing pesticide resistance.

How could information about the toxicity of pesticides to biological control agents best be made available to the end user? How should bioassays be conducted to evaluate pesticide selectivity? There are no simple answers. Data on pesticide toxicity to natural enemies often is buried in publications or reports that pest managers and farmers cannot find easily. Unfortunately, even if the data can be found, it is not easy to interpret bioassay data obtained by different scientists using different methods. Different bioassay methods can produce different conclusions about the toxicity of pesticides to natural enemies, and it is often difficult to predict the effects of pesticides under field conditions based on laboratory assays. Thus, the recommendation that labels or data bases be developed with information on the impact of pesticides on natural enemies requires considerable discussion and additional research. Should pesticide companies conduct the research using standard bioassay methods? Should a consortium of pest management scientists conduct the assays? Who should pay for the research? What species of natural enemies should be tested? This concept is not new; in Europe standardized bioassays already are conducted on selected natural enemy species by a scientific working group concerned about managing pests in glasshouses. Whether this model can be used elsewhere should be explored. Increased international consultation and cooperation between scientists, regulatory agencies, and pesticide companies could resolve many of the questions raised above.

Evolution of pesticide resistance in pests has been shown by computer simulations of predator and prey interactions to be slowed by reduced pesticide use. There is general agreement that reduced pesticide use is one of the essential elements of any resistance management program. Thus, the compatibility of pesticides and biological control agents is a crucial issue in pesticide resistance management.

Attempts to manage pesticide resistance (Table 10) in pest arthropods generally has involved making relatively minor tactical shifts in use patterns. A major shift in how we think about pesticide development and use could provide more effective resistance management tactics. The

Pesticide Resistance Management, Table 10 **Important assumptions of resistance management models; violation of the assumptions could make management decisions based on these models ineffective (modified from Hoy 1998)**

Model type	Assumptions
Mixtures	Resistance to each product is monogenic
	No cross resistance occurs between products in the mixture
	Resistant individuals are rare in the population
	Products have equal persistence
	Some of the population remain untreated (refuge)
	Resistance is functionally recessive (only homozygotes survive exposure)
Mosaics	Susceptible individuals are maintained and able to move into surrounding patches
	Negative cross resistance or fitness costs associated with the resistance may be required
Rotations	The frequency of individuals resistant to one product will decline during application of the alternative product, which is true if there is negative cross resistance (rare), a substantial fitness cost associated with resistance, or immigration of susceptible individuals occurs
High-dose strategy	Assumes complete coverage, effective kill of all individuals, ignores negative effects on secondary pests and their natural enemies or the environment

strategy should be to manage use of the pesticide, even before it is fully developed and registered. If this strategy is adopted, decisions on application rates and the numbers of applications per growing season would be made with the understanding that they affect the speed with which resistance will develop. In some cases, new products may not be registered for specific crops because they are toxic to biological control agents in that crop and thus could disrupt effective IPM programs in place.

Pesticide-Resistant Natural Enemies

Pesticide-resistant natural enemies are a special category of pesticide selectivity. Relatively few natural enemies have developed resistance to pesticides through natural selection, but several have been important in effective IPM programs. Artificial selection of phytoseiid predators for pesticide resistance can be a practical and cost effective tactic for the biological control of spider mites. Field tests have been conducted with several laboratory-selected phytoseiid species and some are being used in IPM programs.

Selection of pesticide-resistant strains of parasitoids and predatory insects have been conducted and some strains have been evaluated for incorporation into IPM programs. The use of mutagenesis and recombinant DNA techniques could improve the efficiency of such genetic improvement projects. However, development of pesticide-resistant natural enemies is time consuming and expensive and should not be considered before exploring other, less expensive, options for IPM and pesticide resistance management.

Pesticides are powerful and effective pest management tools. Some can be highly selective, rapid in their impact, adaptable to many situations, and relatively economical. Thus, preserving pesticides is essential. Effective paradigms for resistance management are not yet deployed because resistance management and IPM have been considered separate issues. Effective programs will acknowledge the role of biological control, host plant resistance, cultural controls, and biorational controls such as mating disruption, insect growth regulators, and mass trapping. A key issue should always be whether pesticides can be used in a precise and selective manner without disrupting natural enemies.

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Pest Resurgence

Increase in abundance of pests, rapidly and sometimes to higher than previous levels, following actions made to suppress them.

Pest Risk Analysis (Assessment)

The process of evaluating biological or other scientific or economic evidence to determine whether a pest should be regulated, and the strength of any regulatory measures to be directed against it.

Biological pollution, the inadvertent introduction or invasion of nonindigenous species, is one of the most serious ecological problems facing contemporary societies. The greatly expanded "free trade" policies of the modern world have greatly exacerbated the problems with alien invasive organisms. Environmental autonomy, or the ability of a nation to protect its own flora and fauna, has usually been relegated to secondary importance; economic benefits seem to be more important than ecological benefits in most areas of the world. There are ample legal grounds for countries to act to protect human, animal or plant life or health, provided that "protective" acts are not economic acts disguised as environmental actions. Thus, there must be ample scientific justification for such protective acts. Pest risk analysis is a means of obtaining objective assessment of the hazards associated with pest introduction.

Pest risk analysis should identify hazards, quantify risks, and identify management options and strategies. The assessment should provide a reasonable estimation of overall risk. The ability of an introduced organism to become established involves a mixture of inherent (biological) and environmental characteristics. There is a great deal of uncertainty associated with such estimates.

Biosecurity hazards can be classified into three groups: vectors, pathways, and species. Vectors are the means of introduction (e.g., fruit or flower contamination). Pathways are the specific routes of introduction; shipping (air or sea transport) usually is implicated. The species of concern may be easily identified in some cases, but often multiple threats exist. For biosecurity hazards to be adequately assessed, the entire suite of vector, pathway, and species issues must be known.

Most hazard identification is calculated deductively. Deductive techniques rely on examination of what has occurred in the past. Though valuable, past experience is not entirely inclusive, and new hazards may exist. Alternatively, inductive techniques are sometimes employed, including logic tree analysis, hazard and operability analysis, and failure modes and effects analysis. These latter techniques help identify possible, though not necessarily probable, events that can be overlooked during deductive assessment because they may have not occurred previously.

Quantifying risks determines the likelihood and consequences of biological pollution. Few quantitative data are available to assist in this process, so it tends to be more qualitative than quantitative. However, quantitative assessments are subject to scientific scrutiny, and so may be "testable," and amenable to revision and improvement. A typical risk assessment model consists of a calculation of the probability of establishment [P] – the product of association with a pathway [Xa], entry potential [Xe], colonization potential [Xc], and spread potential [Xs]): P = [Xa] [Xe] [Xc] [Xs]. The consequences of establishment [C] are calculated by summation of the economic impact potential [X], environmental impact potential [Y], and "perceived impact" (social and political influences) [Z]: C = X + Y + Z.

Ultimately, the goal of pest risk assessment is to manage or eliminate introductions or reduce the rates of invasion. Thus, risk analysis seeks to identify weak links in the invasion sequence, identify where additional information is needed, identify the optimal management processes, and determine the probability and costs of failure.

► Invasive Species

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Pests and their Natural Enemies (Parasitoids and/or Predators) in the Middle East

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The Middle East is a geographic region comprising a territory in which Asia, Africa, and Europe converge and which includes the Mediterranean Sea, the Red Sea, and the Persian Gulf. To the south, the Sahara Desert divides it from Tropical Africa; to the north, its outer limits lie in the latitude of the Black and Caspian Seas. On the east it extends as far as the Indian subcontinent, while its western limits lie at about the longitude of the Aegean Sea.

Agriculture is the most important activity in the Middle East in terms of the number of people it employs; in some countries it provides a substantial part of the gross domestic economy. Rainfed farming is possible only in these limited areas that receive more than 8 inches (800 mm) of rain annually, and then only for winter crops, because the summer is dry everywhere. A perennial supply of irrigation water is available from the Middle East's two great river systems, the Nile in Egypt and the Tigris-Euphrates system in Iraq and Syria. The agriculture these rivers support is highly productive. Irrigation water is also obtainable from underground water resources. These include renewable ground water resources, continually resupplied from precipitation and subterranean flow, and nonrenewable resources such as the fossil water deposits of the Sahara and Arabian peninsula. Another important agricultural resource of the Middle East is the region's grazing lands.

The largest vegetable production area in the world is in Asia, with 61% of total production and an annual growth rate of 5.1% per year. Over 100 types of vegetable crops are grown and consumed. Developing countries account for 61% of world vegetable production. China has the highest proportion of vegetable production, with South Asia is second with 19.4% of developing countries' vegetable production, followed by the Near East (8.5%) and East and South East Asia (9.1%). In terms of income generation, vegetable production has an important economic significance in developing countries. In many developing countries, the return per hectare for vegetable crops is twice the return for rice crops. Small-holder producers with limited mechanization carry out most production. This also increases the opportunities for on-farm employment. In 1996, developing countries accounted for 72% of world fresh fruit production.

According to FAO (1998), citrus is the most important fruit crop with world production at 87 million tons and increasing at an annual rate of 3.4% per year. Bananas are the second most important fruit commodity with 82 million tons and an annual growth increase of 2.7%. Most of the world banana production occurs in the developing countries of Latin America, Asia and Africa. Tomatoes are the third most important crop with 80 million tons of annual production and an annual production increase of 2.9% per year. Grapes are the fourth most important fruit crop with 55 million tons of annual production. Apples are the fifth most important fruit crop with 49 million tons of annual production.

Following is a list of key pests, sorted by crop known to be important in the Middle East. Indented beneath each pest is a list of natural enemies of each pest found in this region, and where they are known to occur.

Key insect and mite pests and their determined natural enemies in the Middle East (natural enemies are indented under their hosts)

a. Information for each crop is arranged as follows: name of the crop; scientific name of pest(s); scientific name of natural enemy(ies) (parasitoid or predator), if available; country where species were encountered and studied.
b. Reference in Arab Journal of Plant Protection.
c. Seventh Arab Congress of Plant Protection. 22–26 October 2000. Amman, Jordan. Abstract Book.
d. Gerling, D. 1990. Whiteflies: their Bionomics, Pest Status and Management.

Alliaceae

Garlic

Thrips tabaci Lindeman (Thysanoptera: Thripidae); Egypt[c], Lebanon

Onion

Thrips tabaci Lindeman (Thysanoptera: Thripidae); Jordan[c], Saudi Arabia

Anacardiaceae

Pistachio Tree

Agonoscena targionii (Licht.) (Hemiptera: Psyllidae)
- *Adonia variegata* Goetze (Coleoptera: Coccinellidae); Lebanon, Syria
- *Anthocorus minki* Dohrm (Hemiptera: Anthocoridae); Syria
- *Camphylomma* sp. (Hemiptera: Miridae); Syria
- *Chilocorus bipustulatus* (L.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
- *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae); Jordan, Syria
- *Coccinella novemnotata* Herbst (Coleoptera: Coccinellidae); Syria
- *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria
- *Coccinella tredecimpunctata* (L.) (Coleoptera: Coccinellidae); Syria
- *Coccinella undecimpunctata* (L.) (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria
- *Geocoris* sp. (Hemiptera: Lygaeidae); Syria
- *Hyperaspis quadrimaculatus* Redt. (Coleoptera: Coccinellidae); Syria, Turkey
- *Nabis ferrus* L. (Hemiptera: Nabidae); Syria

Orius horvathi (Reuter) (Hemiptera: Anthocoridae); Syria

Psyllaephagus pistaciae (Hymenoptera: Encyrtidae); Syria

Rhizophagus sp. (Coleoptera: Rizophagidae); Syria

Scymnus sp. (Coleoptera: Coccinellidae); Syria

Stethorus sp. (Coleoptera: Coccinellidae); Syria

Syrphus sp. (Diptera: Syrphidae); Lebanon, Syria

Capnodis cariosa Pall. (Coleoptera: Buprestidae); Lebanon, Syria

Hylesinus vestitus M. & R. (Coleoptera: Curculionidae: Scolytinae); Syria[c]

Cheiropachus quadrum F. (Hymenoptera: Pteromalidae); Syria

Clerus mutillarius Fisch. (Coleoptera: Cleridae); Syria

Dendrosoter protuberans (Nees) (Hymenoptera: Braconidae); Syria

Denops albofasciata K. (Coleoptera: Cleridae); Syria

Iponemus sp. (Acari: Tarsonemidae); Syria, Lebanon, Turkey

Tarsonemus sp. (Acari: Tarsonemidae); Syria

Thanasimus formicarius (L.) (Coleoptera:Cleridae); Syria

Thaumetopoea solitaria (Fr.) (Lepidoptera: Thaumetopoeidae); Iraq, Iran, Lebanon, Syria, Turkey

Arecaceae/Palmae

Palm

Apate monachus F. (Coleoptera: Bostrychidae); Algeria[c]

Arenipses sabella Hampson (Lepidoptera: Pyralidae); Algeria, Iran, Iraq, Libya, Saudi Arabia

Batrachedra amydraula Meyrick (Lepidoptera: Cosmopterygidae); Egypt, Iraq, Libya, Saudi Arabia

Ecotomyelois ceratoniae (carob moth)

Habrobracon hebetor Say (Hymenoptera: Braconidae); Tunisia[c]

Ephestia cautella (Walker) (Lepidoptera:Pyralididae); Iraq and Libya[c]

Bracon hebetor Say. (Hymenoptera: Braconidae); Iraq[c]

Icerya purchasi Mask. (Hemiptera: Margarodidae); Libya

Jebusea hammerschmidti Reiche (Coleoptera: Cerambycidae); Iraq, Saudi Arabia

Ommatissus binotatus Berg. (Hemiptera: Tropiduchidae); Algeria, Egypt, Libya

Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae); Iraq

Chrysopa carnea Steph. (Neuroptera: Chrysopidae); Iraq

Coccinella septempunctata L. (Coleoptera: Coccinellidae); Iraq

Coccinella undecimpunctata L. (Coleoptera: Coccinellidae); Iraq

Oryctes elegans Prell (Coleoptera: Scarabaeidae); Iraq[c] & Qatar[c], Saudi Arabia

Paratetranychus afrasiaticus (McG.) (Acari: Tetranychidae); Saudi Arabia

Parlatoria blanchardi Targioni-Tozzetti (Hemiptera: Diaspididae); Egypt, Iran, Iraq[b], Jordan, Libya, Palestine, Saudi Arabia

Phoenococcus marlatti Cock (Hemiptera: Phoenicococcidae); Libya

Phonapate frontalis Farhr. (Coleoptera:Bostrychidae); Iraq, Libya, Saudi Arabia

Planococcus citri (Risso) (Hemiptera: Pseudococcidae); Libya

Pseudophilus testaceus Gahan (Coleoptera: Curculionidae); Iraq & Qatar[c]

Rhynchophorus ferrugineus Fabricius (Coleoptera: Curculionidae); Egypt[c], Qatar[c], & Saudi Arabia

Schistocerca gregaria Forsk. (Orthoptera: Acrididae); Iraq, Jordan, Lebanon, Libya, Palestine, Saudi Arabia, Syria, Turkey

Brassicaceae (Cruciferae)

Cabbage

Aporia crataegi (L.) (Lepidoptera: Pieridae)

Apanteles (*Cotesia*) *glomeratus* L. (Hymenoptera: Braconidae); Lebanon, Syria

Bemisia tabaci Genn. (Hemiptera/Hemiptera: Aleyrodidae)

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[c]

Brevicoryne brassicae L. (Hemiptera: Aphididae)
Aphidius brassicae March. (Hymenoptera: Braconidae); Lebanon
Diaeretiella rapae Mc' Intosh (Hymenoptera: Braconidae); Jordan, Lebanon, Syria
Pieris brassicae L. (Lepidoptera: Pieridae)
Cotesia glomeratus L. (Hymenoptera: Braconidae); Lebanon, Syria
Brachymeria intermedia Nees (Hymenoptera: Chalcididae); Lebanon
Compsilura sp. (Diptera: Tachinidae); Syria
Hyposoter sp. (Hymenoptera: Ichneumonidae); Syria
Spodoptera littoralis (Boisd.) (Lepidoptera: Noctuidae); Egypt, Lebanon, Iraq[b]

Cauliflower

Bemisia tabaci Genn. (Hemiptera: Aleyrodidae)
Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[b]
Spodoptera littoralis Boisduval (Lepidoptera: Noctuidae); Iraq[b]

Kohlrabi (*Brassica oleraceae* var. *caularapa*)

Atherigona orientalis (Schinner) (Diptera: Muscidae); Iraq[b]
Baris opiparis Jacquilin DuVal (Coleoptera: Curculionidae); Iraq[b]
Hellula undalis (Fabricius) (Lepidoptera: Pyralidae); Iraq[b]

Chenopodiaceae

Sugarbeet

Agrotis segetum (Schiff) (Lepidoptera: Noctuidae); Lebanon, Syria
Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae); Lebanon, Iraq, Syria

Cucurbitaceae

Cucumber

Aphis gossypii Glover (Hemiptera: Aphididae)
Aphidius colemani Vierck (Hymenoptera: Aphidiidae); Algeria[c], Egypt[c], Lebanon, Saudi Arabia, Syria
Bemisia tabaci Genn. (Hemiptera: Aleyrodidae); Egypt[c], Lebanon, Syria[b]
Empoasca decipiens Paoli (Hemiptera: Cicadellidae); Egypt[c], Jordan, Lebanon, Syria
Henosepilachna elaterii Rossi (Coleoptera: Coccinellidae); Sudan[b]
Liriomyza cicerina Rond. (Diptera: Agromyzidae)
Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria
Liriomyza huidobrensis (Blanchard) (Diptera: Agromyzidae)
Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria
Hemiptarsenus sp. (Hymenoptera: Eulophidae); Syria
Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae); Jordan, Lebanon, Syria
Halticoptera sp. (Hymenoptera: Pteromalidae); Syria
Liriomyza trifolii (Burgess) (Diptera: Agromyzidae)
Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria
Tetranychus urticae Koch (Acari: Tetranychidae)
Phytoseiulus persimilis (Acarina: Phytoseiidae); Lebanon & Syria[b]
Thrips tabaci Lindeman (Thysanoptera: Thripidae); Egypt[c], Syria[b]
Trialeurodes vaporariorum Westwood (Hemiptera: Aleyrodidae); Syria[b]

Melon

Acytopeus (Baris) curvirostris (Tourn.) (Coleoptera: Curculionidae)
Sarcophaga sp. (Diptera: Sarcophagidae); Saudi Arabia
Aphis gossypii Glover (Hemiptera: Aphididae)
Aphelinus gossypii (Timberlake) (Hymenoptera: Aphelinidae); Jordan[c], Lebanon, Syria

Dacus ciliatus Lw. (Diptera: Tephritidae); Egypt Lebanon, Saudi Arabia, Syria, Sudan

Eudioptes (Margaronia) indica Sn. (Lepidoptera: Pyralidae); Saudi Arabia, Syria

Myopardalis pardalina Bigot (Diptera: Tephritidae); Lebanon, Syria

Squash

Aphis gossypii Glover (Hemiptera: Aphididae); Egypt[c], Lebanon, Syria

Bemisia tabaci Genn. Genn. (Hemiptera: Aleyrodidae); Egypt[c], Lebanon, Syria

Empoasca decipiens Paoli (Hemiptera: Cicadellidae); Egypt[c], Lebanon, Syria

Watermelon

Acytopeus (Baris) curvirostris (Tourn.) (Coleoptera: Curculionidae)

- *Sarcophaga* sp. (Diptera: Sarcophagidae); Saudi Arabia

Aphis gossypii Glover (Hemiptera: Aphididae)

- *Aphelinus gossypii* (Timberlake) (Hymenoptera: Aphelinidae); Jordan[c], Lebanon, Syria

Trichoplusia ni (Hübner) (Lepidoptera: Noctuidae); Lebanon

Fagaceae

Cork oak

Cerambyx cerdo L. (Coleoptera: Cerambycidae); Algeria[c]

Platypus cylindrus F. (Coleoptera: Platypodidae); Algeria[c]

Oak

Malacosoma neustria L. (Lepidoptera: Lasiocampidae); Libya[c]

Gramineae/Poaceae

Barley

Cephus pygmaeus L. (Hymenoptera: Cephidae)

- *Collyria coxator* Villers (Hymenoptera: Ichneumonidae); Syria[b]
- *Collyria orientator* Aubert (Hymenoptera: Ichneumonidae); Syria[b]
- *Bracon terebrella* Wesmael (Hymenoptera: Braconidae); Syria[b]

Cnephasia pumicana Zeller (Lepidoptera: Tortricidae); Syria[c]

Diuraphis noxia Kurdjumov (Hemiptera: Aphididae)

- *Syrphus* sp. (Diptera: Syrphidae); Syria[b]
- *Leucopis* sp. (Diptera: Chamaemyiidae); Syria[b]
- *Coccinella septempunctata* L. (Coleoptera: Coccinellidae); Syria[b]
- *Diaretiella rapae* (Hymenoptera: Aphidiidae); Syria[b]
- *Praon* sp. (Hymenoptera: Aphidiidae); Syria[b]
- *Aphidius colemani* (Hymenoptera: Aphidiidae); Syria[b]

Eurygaster integriceps Puton (Hemiptera: Scutelleridae); Iran[b], Iraq, Syria[c], Turkey

- *Asolcus* sp. (Hymenoptera, Scelionidae); Iran, Syria
- *Microphanurus vasilievi* (Mayr) (Hymenoptera); Iran, Syria

Haplothrips tritici Kurd (Thysanoptera: Phlaeothripidae); Syria[c]

Oria musculosa Hübner (Lepidoptera: Noctuidae); Syria[c]

Porphyrophora tritici Bodenheimer (Hemiptera: Margarodidae); Syria[b]

Rhopalosiphum maidis Fitch (Hemiptera:Aphididae); Iraq, Lebanon, Syria[c]

Rhopalosiphum padi L. (Hemiptera: Aphididae); Iraq[b]

Schizaphis graminum (Rondani) (Hemiptera: Aphididae); Iraq

Sitotroga cerealella (Olivier) (Lepidoptera: Gelechiidae); Iraq

Tracheus judaicus Konow (Hymenoptera: Cephidae)

- *Collyria coxator* Villers (Hymenoptera: Ichneumonidae); Syria[b]
- *C. orientator* Aubert (Hymenoptera: Ichneumonidae); Syria[b]

Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Trachelus libanensis Andre (Hymenoptera:Cephidae)

Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]

C. orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]

Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Corn

Cicadulina chinai Ghauri (Hemiptera: Cicadellidae); Egypt[c]

Cicadulina bipuncellazea China (Hemiptera: Cicadellidae); Egypt[c]

Empoasca descipiens Paoli (Hemiptera: Cicadellidae); Egypt[c], Jordan, Lebanon, Syria

Empoasca decedens Paoli (Hemiptera: Cicadellidae); Egypt[c]

Ostrinia (Pyrausta) *nubilalis* (Hübner) (Lepidoptera: Pyrlidae); Lebanon

Sogatella vibix (Haupt) (Hemiptera: Delphacidae); Egypt[c]

Sogatella furicifera Horv (Hemiptera: Delphacidae); Egypt[c]

Rhopalosiphum maidis Fitch (Hemiptera: Aphididae)

Coccinella septempuncata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Saudi Arabia, Syria

Sesamia cretica Led. (Lepidoptera: Agrotidae); Jordan, Saudi Arabia

Bracon spp. (Hymenoptera: Braconidae); Iraq, Syria

Coccinella septempuncata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria

Coccinella undecimpuncata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria

Orius albidepennis (Reut.) (Hemiptera: Anthocoridae); Iraq

Platytelenomus hylas Nixon (Hymenoptera: Scelionidae); Egypt[c]

Telenomus sp. (Hymenoptera: Scelionidae); Iraq

Tribolium castaneum (Herbst) (Coleoptera: Tenebrionidae)

Platytelenomus hylas Nixon (Hymenoptera: Scelionidae); Iraq[b]

Rice

Sitophilus oryzae L. (Coleoptera: Curculionidae); Iraq[b]

Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Sorghum

Atherigona yorki Deeming (Diptera: Muscidae); Yemen[b]

Chilo partellus Swinhoe (Lepidoptera: Pyralidae); Yemen[b]

Sesamia cretica Lederer (Lepidoptera: Noctuidae); Yemen[b]

Sugarcane

Chilo agamemnon Bleszynski (Lepidoptera: Pyralidae)

Trichogramma evanescens West. (Hymenoptera: Tricogrammatidae); Egypt[b]

Wheat

Cephus pygmaeus L. (Hymenoptera: Cephidae)

Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]

Collyria orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]

Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Diuraphis noxia (Mordvilko) (Hemiptera: Aphididae)

Coccinella septempuncata L. (Coleoptera: Coccinellidae); Lebanon and Syria[b]

Leucopis sp. (Chamaemiiydae: Diptera); Lebanon, Syria

Syrphus sp. (Diptera: Syrphidae); Lebanon, Syria

Aphidius colemani Viereck (Hymenoptera: Braconidae); Lebanon, Syria

Diaeretiella rapae Mc' Intosh (Hymenoptera: Braconidae); Jordan, Lebanon, Syria

Praon sp. (Hymenoptera: Braconidae); Lebanon, Syria

Eurygaster integriceps Puton (Hemiptera: Scutelleridae); Iraq, Lebanon, Turkey

Asolcus sp. (Hymenoptera: Scelionidae); Iran, Syria
Microphanurus vasilievi (Mayr) (Hymenoptera); Iran, Syria
Trissolcus sp. (Hymenoptera: Scelionidae); Syria[c]

Exaeretopus tritici Williams (Hemiptera: Coccidae); Iraq[b]

Lytta vesicatoria (L.) (Coleoptera: Meloidae); Algeria[c]

Mayetiola destructor (Say) (Diptera: Cecidomyiidae); Morocco, Tunisia[c]

Metopolophium dirhodum (Walker) (Hemiptera: Aphididae)
Coccinella septempuncata L. (Coleoptera: Coccienllidae); Lebanon, Syria

Oria musculosa Hübner (Lepidoptera: Noctuidae); Syria

Oulema melanopus (L.) (Coleoptera: Chrysomelidae); Syria[b]

Rhopalosiphum padi (L.) (Hemiptera: Aphididae)
Coccinella septempuctata L. (Coleoptera: Coccinellidae); Syria[c]
Harmonia axyridis Pallas (Coleoptera: Coccinellidae); Syria[c]

Sitobion avenae (Fabricius) (Hemiptera: Aphididae)
Coccinella septempuncata L. (Coleoptera: Coccinellidae); Lebanon, Syria

Trachelus judaicus Konow (Hymenoptera: Cephidae)
Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]
Collyria orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]
Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Trachelus libanensis Andre (Hymenoptera: Cephidae)
Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]
Collyria orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]
Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Leguminoseae

Alfalfa

Sitona discoideus Gyllenhal (Coleoptera: Curculionidae)
Anaphes diana (Girault) (Hymenoptera: Mymaridae); Syria

Sitona lineatus (L.) (Coleoptera: Curculionidae); Lebanon, Syria

Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae)
Chrysopa vulgaris L. (Hymenoptera: Chrysopidae); Libya[b]
Coccinella novemnotata Herbst (Coleoptera: Coccinellidae); Libya[b]
Coccinella septumpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Coccinella undecimpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Hippodamia tredecimpunctata tibialis (Say) (Coleoptera: Coccinellidae); Libya[b]
Nabis ferrus L. (Hemiptera: Nabidae); Libya[b]
Syrphus corollae Fabricius (Diptera: Syrphidae); Libya[b]
Tripolitanus sp. (Diptera: Asilidae); Libya[b]

Spodoptera littoralis (Boisd.) (Lepidoptera: Noctuidae); Egypt, Iraq, Lebanon, Saudi Arabia, Syria

Therioaphis maculata (Buckton) (Hemiptera: Aphididae)
Chrysopa vulgaris L. (Hymenoptera: Chrysopidae); Libya[b]
Coccinella novemnotata Herbst (Coleoptera: Coccinellidae); Libya[b]
Coccinella septumpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Hippodamia tredecimpunctata (L.) (Coleoptera: Coccinellidae); Libya[b]
Coccinella undecimpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Nabis ferrus L. (Hemiptera: Nabidae); Libya[b]
Syrphus corollae Fabricius (Diptera: Syrphidae); Libya[b]
Tripolitanus sp. (Diptera: Asilidae); Libya[b]

Therioaphis trifolii Monell (Hemiptera: Aphididae)
Aphelinus asychis Walker (Hymenoptera: Aphelinidae); Syria
Aphelinus semiflavus Howard (Hymenoptera: Aphelinidae); Syria
Coccinella septumpunctata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria
Malacocoris sp. (Hemiptera: Miridae); Syria
Praon exoletum (Needs) (Hymenoptera: Aphidiidae); Lebanon, Syria

Praon palitans Muesebeck (Hymenoptera: Aphidiidae); Lebanon, Palestine, Saudi Arabia

Trioxys complanatus Quilis Pérez (Hymenoptera: Aphidiidae); Lebanon

Trioxys utilis Muesebeck (Hymenoptera: Aphidiidae); Lebanon, Palestine, Syria

Beans

Aphis craccivora Koch (Hemiptera: Aphididae); Egypt[b]

Aphis fabae Scopoli (Hemiptera: Aphididae)

Coccinella septempunctata L. (Coleoptera: Coccinellidae); Syria[c]

Harmonia axyridis Pallas (Coleoptera: Coccinellidae); Syria[c]

Chrysoperla carnea (Stephens) (Neuroptera: Chrysopidae); Jordan, Syria

Didea sp. (Diptera: Syrphidae); Syria

Epistrophella sp. (Diptera: Syrphidae); Syria

Episyrphus balteatus De Geer (Diptera: Syrphidae); Lebanon, Syria

Eristalis sp.; Syria

Lysiphlebus confusus Tremblay & Eady (Hymenoptera: Aphidiidae); Lebanon

Melanostoma sp. (Diptera: Syrphidae); Syria

Scaeva sp. (Diptera: Syrphidae); Syria

Scymnus apetzi Mulsant (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Trioxys angelicae (Haliday) (Hymenoptera: Aphidiidae); Lebanon

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae); Iraq, Jordan, Lebanon

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[c]

Liriomyza cicerina Rondani (Diptera: Agromyzidae)

Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Liriomyza huidobrensis (Blanchard) (Diptera: Agromyzidae)

Chrysocharis orbicularis (Nees) (Hymenoptera: Eulophidae); Lebanon

Crossopalpus sp. (Diptera: Empididae); Syria

Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Halticoptera sp. (Hymenoptera: Pteromalidae); Syria

Hemiptarsenus sp. (Hymenoptera: Eulophidae); Syria

Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae); Jordan, Lebanon, Syria

Nordlanderia sp. (Hymenoptera: Eucoilidae); Lebanon

Opius sp. (Hymenoptera: Braconidae); Syria

Pediobius acantha (Walker) (Hymenoptera: Eulophidae); Syria

Platypalpus sp. (Diptera: Empididae); Syria

Liriomyza trifolii (Burgess) (Diptera: Agromyzidae)

Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Lixus algirus L. (Coleoptera: Curculionidae); Syria[b]

Melanagromyza (*Agromyza*) *phaseoli* Coq. (Diptera: Agromyzidae); Lebanon

Rhopalosiphum padi L. (Hemiptera: Aphididae)

Coccinella septempuctata L. (Coleoptera: Coccinellidae); Syria[c]

Harmonia axyridis Pallas (Coleoptera: Coccinellidae); Syria[c]

Sitona crinitus H. (Coleoptera: Curculionidae); Syria[c]

Tetranychus urticae Koch (Acari: Tetranychidae)

Phytoseiulus persimilis (Acarina: Phytoseiidae); Lebanon & Syria[b]

Trialeurodes ricini Misra (Hemiptera: Aleyrodidae)

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Jordan[c]

Chickpeas

Heliocoverpa (*Heliothis*) *armigera* Hb. (Lepidoptera: Noctuidae); Jordan, Lebanon

Cynopterus sp. (Hymenoptera: Braconidae); Syria

Bracon hebetor (Say.) (Hymenoptera: Braconidae); Iraq, Syria

Campoletis sp. (Hymenoptera: Ichneumonidae); Syria

Liriomyza cicerina Rondani (Diptera: Agromyzidae)

Opius sp. (Hymenoptera: Braconidae); Syria

Dygliphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Lixus algirus L. (Coleoptera: Curculionidae); Syria[b]

Sitona lineatus (L.) (Coleoptera: Curculionidae); Lebanon, Syria[b]

Lentils

Heliothis spp. (Lepidoptera: Noctuidae); Syria[b]

Liriomyza cicerina Rondani (Diptera: Agromyzidae); Syria[b]

Lixus algirus L. (Coleoptera: Curculionidae); Syria[b]

Sitona lineatus (L.) (Coleoptera: Curculionidae); Lebanon, Syria[b]

Smynthurodes betae Westwood (Hemiptera: Aphididae)

- *Chrysotoxum intermedium* Meigen (Diptera: Syrphidae); Syria, Turkey
- *Hyperaspis quadrimaculatus* Redt. (Coleoptera: Coccinellidae); Syria, Turkey

Soybeans

Aphis gossypii (Glover) (Hemiptera: Aphididae); Egypt[b]

Bemisia tabaci Gennadius (Hemiptera: Aleyrodidae); Egypt[b]

Earias insulana Boisduval (Lepidoptera: Noctuidae); Egypt[b]

Empoasca lybica De Bergevin (Hemiptera: Cicadellidae); Egypt[b]

Platyedra (*Pectinophora*) *gossypiella* (Saunders) (Lepidoptera: Gelechiidae); Egypt[b]

Spodoptera littoralis Boisduval (Lepidoptera: Noctuidae); Egypt[b]

Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae); Egypt[b]

Lythracaea

Pomegranate

Aphis punicae Passerini (Hemiptera: Aphididae)

- *Aphidius* sp. (Hemiptera: Aphidiidae); Libya[c]
- *Coccinella novemnotata* Herbst (Coleoptera: Coccinellidae); Libya[c]
- *Scymnus nubilus* Mulsant (Coleoptera: Coccinellidae); Libya[c]
- *Scymnus syriacus* Mars. (Coleoptera: Coccinellidae); Libya[c]
- *Syrphus corollae* Fab. (Diptera: Syrphidae); Libya[c]

Ectomyelois ceratoniae Zeller (Lepidoptera: Pyralidae)

- *Apanteles angaleti* Muesebeck (Hymenoptera: Braconidae); Iraq[c]

Siphoninus phillyreae (Haliday) (Hemiptera: Aleyrodidae)

- *Eretmocerus* sp. (Hymenoptera: Aphelinidae); Jordan, Syria
- *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae); Jordan, Syria

Tenuipalpus punicae P. & B. (Acari: Tenuipalpidae); Iraq[b]

Virachola (Deudorix) livia Klug (Lepidoptera: Lycaenidae)

- *Brachymeria* sp. (Hymenoptera: Chalcididae); Jordan

Malvaceae

Cotton

Aphis gossypii Glov. (Hemiptera: Aphididae)

- *Aphelinus gossypii* (Temberlack) (Hymenoptera: Aphelinidae); Jordan
- *Geocoris megacephalus* (Rossi) (Hemiptera: Lygaeidae); Syria
- *Hyperaspis variegata* Goeze (Coleoptera: Coccinellidae); Lebanon
- *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae); Syria
- *Scymnus levaillanti* Mulsant (Coleoptera: Coccinellidae); Jordan, Syria
- *Scymnus quadriguttatus* Capra (Coleoptera: Coccinellidae); Syria
- *Scymnus subvillosus* (Goeze) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
- *Trioxys angelicae* (Haliday) (Hymenoptera: Aphidiidae); Lebanon

Bemisia tabaci Gennadius; Egypt[c]

- *Campylomma diversicornis* Reuter (Hemiptera: Miridae); Syria
- *Deraeocoris punctulatus* (Fallen) (Hemiptera: Miridae); Syria
- *Encarsia lutea* (Masi) (Hymenoptera: Aphelinidae); Jordan, Syria
- *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae); Jordan, Syria
- *Macrolophus* sp. (Hemiptera: Miridae); Syria

Earias insulana Boisduval (Lepidoptera: Noctuidae); Egypt[b], Iraq, Iran, Turkey

Trichogramma brassicae Bezdenko (Hymenoptera: Trichogrammatidae); Syria

Helicoverpa armigera Hübner (Lepidoptera: Noctuidae)

Bracon (*Haprobracon*) *brevicornis* Wesmael (Hymenoptera: Braconidae); Syria

Haprobracon hebetor Say (Hymenoptera: Braconidae); Syria

Trichogramma brassicae Bezdenko (Hymenoptera: Trichogrammatidae); Syria

Trichogramma chilonis Ishii (Hymenoptera: Trichogrammatidae); Syria

Trichogramma principium Sugonyaev-Sorokina (Hymenoptera: Trichogrammatidae); Syria

Platyedra (*Pectinophora*) *gossypiella* (Saunders) (Lepidoptera: Gelechiidae); Egypt[b], Sudan, Syria

Spodoptera litoralis Boisduval (Lepidoptera: Noctuidae); Eygpt[b]

Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae)

Chrysoperla carnea (Stephens) (Neuroptera: Chrysopidae); Syria

Exochomus pubscens Kuster (Coleoptera: Coccinellidae); Jordan

Okra

Bemisia tabaci Gennadius. (Hemiptera: Aleyrodidae)

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[c]

Earias insulana Boisduval (Lepidoptera: Noctuidae); Lebanon, Saudi Arabia

Oleaceae

Olives

Acaudaleyrodes olivinus Silvestri (Hemiptera: Aleyrodidae)

Encarsia spp.; Jordan

Bactrocera (*Dacus*) *oleae* Gmelin (Diptera: Tephritidae); Libya[c]

Carpophilus mutilatus Er. (Coleoptera: Nitidulidae); Lebanon

Cyrtoptyx dacicida Masi (Hymenoptera: Pteromalidae); Lebanon

Cyrtoptyx latipes (Rondani) (Hymenoptera: Pteromalidae); Egypt[c]

Eupelmus sp. (Hymenoptera: Eupelmidae); Egypt[c]

Eupelmus urozonus Dal. (Hymenoptera: Eupelmidae); Lebanon

Eurytoma rosae Nees (Hymenoptera: Eurytomidae); Lebanon

Eurytoma martelli M. (Hymenoptera: Eurytomidae); Egypt[c], Syria

Macroneura sp. (Hymenoptera: Eupelmidae); Egypt[c]

Opius concolor Szépligeti (Hymenoptera: Braconidae); Egypt[c],Lebanon, Palestine, Syria

Platygaster sp. (Hymenoptera: Scelionidae); Lebanon

Pnigalio agraules W. (Hymenoptera: Eulophidae); Egypt[c]

Pnigalio mediterraneus Ferriere & Delucchi (Hymenoptera: Eulophidae); Lebanon, Syria

Prolasioptera berlesiana Paoli (Diptera: Cecidomyidae); Lebanon

Synopeas sp. (Hymenoptera: Scelionidae); Lebanon

Clinodiplosis oleisuga Targ. (Diptera: Cecidomyiidae)

Inostema sp. (Hymenoptera: Platygasteridae); Syria, Jordan, Lebanon

Leptacis sp. (Hymenoptera: Platygasteridae); Syria

Dasyneura (*Perrisia*) *oleae* (Loew) (Diptera: Cecidomyiidae)

Aprostocetus sp. (Hymenoptera: Eulophidae); Jordan, Lebanon

Platygaster apicalis Thomas; Syria

Platygaster oleae Szeleny; Jordan, Syria

Euphyllura straminea Loginova (Hemiptera: Psyllidae)

Anthocoris nemoralis (Fabricius) (Hemiptera: Anthocoridae); Syria

Anthocoris nomorum L. (Hemiptera: Anthocoridae); Lebanon, Syria

Crysoperla carnea (Stephens) (Neuroptera: Chrysopidae); Jordan, Lebanon, Syria

Euphyllura olivina Costa (Hemiptera: Psyllidae)

Anthocoris nemoralis (Fabricius) (Hemiptera: Anthocoridae); Syria

Anthocoris nomorum L. (Hemiptera: Anthocoridae); Lebanon, Syria

Parlatoria oleae (Clovée) (Hemiptera: Diaspididae)

Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae; Jordan, Lebanon, Syria

Phloeotribus scarabeoides (Bern.) (Coleoptera: Curculionidae: Scolytinae); Lebanon, Morocco[c], Syria

Prays oleellus F. (Lepidoptera: Hyponomeutidae)

Ageniaspis fuscicollis (Dalman) (Hymenoptera: Encyrtidae); Lebanon

Apanteles dilectus Haliday (Hymenoptera: Braconidae); Lebanon

Chelonus elaeaphilus Silv. (Hymenoptera: Braconidae); Lebanon

Chrysocharis sp. (Hymenoptera: Eulophidae); Lebanon

Cirrospilus elongatus Boucek (Hymenoptera: Eulophidae); Lebanon

Elasmus flabellatus Fonscolombe (Hymenoptera: Elasmidae); Lebanon

Himertosoma sp. Schmiedeknecht (Hymenoptera: Ichneumonidae); Syria

Phytomyptera sp. Rond. (Diptera: Tachinidae); Lebanon

Trichogramma oleae Voegelé-Pointel (Hymenoptera: Trichogrammatidae); Syria

Saissetia oleae (Bern.) (Hemiptera: Coccidae)

Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Scutellista cyanea Motschulsky (Hymenoptera: Ormyridae); Lebanon, Syria

Pedaliaceae

Sesame

Asphondylia sesami Felt (Diptera: Cecidomyiidae); Yemen[b]

Antigastra catalaunalis Duponchel (Lepidoptera: Pyralidae); Yemen[b]

Pinaceae

Cedars

Cephalcia tannourinensis Chevin (Hymenoptera: Pamphiliidae); Lebanon

Dasineura cedri Coutin (Diptera: Cecidomyiidae); Lebanon

Thaumetopoea pityocampa Schiff. (Lepidoptera: Thaumetopoeidae)

Anastatus bifasciatus Fonsc. (Hymenoptera: Eupelmidae); Lebanon, Morocco[b]

Baryscapus (*Tetrastichus*) *servadeii* (Dom.) (Hymenoptera: Eulophidae); Lebanon, Morocco[b]

Ooencyrtus pityocampae Mercet (Hymenoptera: Encyrtidae); Lebanon, Morocco[b]

Trichogramma embryophagum Hartig (Hymenoptera: Trichogrammatidae); Morocco[b]

Pine

Aspidiotes hederae (Vallot) (Hemiptera: Diaspididae)

Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Eulachnus rileyi (Williams) (Hemiptera: Lachnidae); Iraq[b]

Thaumetopoea pityocampa (Den. and Schiff.) (Lepidoptera: Thaumetopoeidae)

Anastatus bifasciatus Fonsc. (Hymenoptera: Eupelmidae); Morocco[b]

Baryscapus (*Tetrastichus*) *servadeii* (Domenichini) (Hymenoptera: Eulophidae); Syria[c]

Calosoma sycophanta L. (Coleoptera: Carabidae); Lebanon, Syria

Ooencyrtus pityocampae (Mercet) (Hymenoptera: Encyrtidae); Morocco[b], Syria[c]

Phryxe caudata (Rondani) (Diptera: Tachinidae); Syria

Trichogramma embryophagum Hartig. (Hymenoptera: Trichogrammatidae); Morocco[b], Syria[c]

Thaumetopoea wilkinsoni Tams. (Lepidoptera: Thaumetopoeidae)

Anastatus bifasciatus Fonsc. (Hymenoptera: Eupelmidae); Lebanon[c]

Baryscapus (*Tetrastichus*) *servadeii* (Domenichini) (Hymenoptera: Eulophidae); Lebanon

Compsilura concinnata (Meigen) (Diptera: Tachinidae); Lebanon

Ooencyrtus pityocampae (Mercet) (Hymenoptera: Encyrtidae); Lebanon

Phryxe caudata (Rondani) (Diptera: Tachinidae); Lebanon

Rosaceae

Almond

Aporia crataegi L. (Lepidoptera: Pieridae)

Apanteles glomeratus (L.) (Hymenoptera: Braconidae); Lebanon, Syria

Microbracon kikpatricki Wilk. (Hymenoptera: Braconidae); Syria

Trichogramma semblidus (Aurivilius) (Hymenoptera: Trichogrammatidae); Syria

Brachycaudus amygdalinus (Schout.) (Hemiptera: Aphididae)

Aphidius matricariae Hal. (Hymenoptera: Aphidiidae); Lebanon, Syria

Aphidoletes aphidimyza (Rondani) (Diptera: Cecidomyiidae); Lebanon, Syria

Deraeocoris pallens (Reuter) (Hemiptera: Miridae); Lebanon

Exochomus quadripustulatus (L.) (Coleoptera: Coccinellidae); Lebanon, Syria

Leucopis sp. (Diptera: Chamaemyiidae); Lebanon, Syria

Scymnus subvillosus (Goeze) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Synharmonia conglobata (L.) (Coleoptera: Coccinellidae); Lebanon, Syria

Cimbex quadrimaculatus Muell. (Hymenoptera: Tenthredinidae); Cyprus, Lebanon, Syria, Turkey

Spilocryptis cimbicis Tschek. (Hymenoptera: Ichneumonidae); Palestine

Eriogaster amygdali talhouki Wilts. (Lepidoptera: Lasiocampidae); Lebanon

Eurytoma amygdali End. (Hymenoptera: Eurytomidae); Palestine

Ascogaster sp. (Hymenoptera: Braconidae); Syria

Mesochorus nigripes Ratz. (Hymenoptera: Ichneumonidae); Syria

Plastotorymus amygdali n.sp. (Hymenoptera: Torymidae); Jordan, Syria

Saltis sp. (Araneae); Lebanon

Syntomaspis sp. (Hymenoptera: Torymidae); Syria

Neurotoma nemoralis L. (Hymenoptera: Pamphiliidae)

Sinophorus (*Limnerium*) *crassifemur* (Thomson) (Hymenoptera: Ichneumonidae); Syria

Pterochloroides persicae (Cholod) (Hemiptera: Lachnidae); Lebanon, Syria

Pauesia sp. (Hymenoptera: Braconidae); Yemen[b]

Apple

Aphis pomi DeGeer (Hemiptera: Aphididae)

Adalia bipunctata (L.) (Coleoptera: Coccinellidae); Lebanon, Jordan, Syria

Adalia decempunctata (L.) (Coleoptera: Coccinellidae); Lebanon, Syria

Harmonia quadripunctata (Melsheimer) (Coleoptera: Coccinellidae); Jordan

Bryobia sp. (Acari: Tetranychidae)

Typhlodromus kettanehi Dosse (Acari: Phytoseiidae); Lebanon

Capnodis tenebrionis L. (Coleoptera: Buprestidae); Lebanon

Cenopalpus pulcher (Canestrini and Fanzago) (Acari: Tenuipalpidae)

Amblyseius finlandicus Ondemans (Acari: Phytoseiidae); Lebanon[b]

Phytoseius ocellatus Bayan (Acari: Phytoseiidae); Lebanon[b]

Typhlodromus invectus Chant (Acari:Phytoseiidae); Lebanon[b]

Typhlodromus kettanehi Dosse (Acari:Phytoseiidae); Lebanon[b]

Typhlodromus pyri Scheuten (Acari:Phytoseiidae); Lebanon[b]

Ceratitis capitata Weid. (Diptera: Tephritidae); Jordan, Lebanon, Syria[c]

Cydia pomonella L. (Lepidoptera: Olethreutidae)

Ascogaster quadridentata Wesml. (Hymenoptera: Braconidae); Syria[c]

Dibrachys cavus (Walker) (Hymenoptera: Pteromalidae); Lebanon

Itoplectis maculator F. (Hymenoptera: Ichneumonidae); Syria[c]

Liotryphon caudatus Ratz. (Hymenoptera: Ichneumonidae); Syria[c]

Microdus rufipes Nees (Hymenoptera:Braconidae); Syria[c]

Perilampus sp. (Hymenoptera: Perilampidae); Lebanon

Perilampus tritis Mayr (Hymenoptera: Perilampidae); Syria[c]

Pristomerus vulnerator Gravenhorst (Hymenoptera: Ichneumonidae); Syria[c]

Trichogramma sp. (Hymenoptera: Trichogrammatidae); Syria[c]

Trichomma enecator Rossi (Hymenoptera: Ichneumonidae); Syria[c]

Dysaphis plantaginea (Passerini) (Hemiptera: Aphididae); Lebanon

Dysaphis pyri Boy. (Hemiptera: Aphididae); Iraq[b]

Eriosoma lanigerum Hausm (Hemiptera:Aphididae)

Adalia bipunctata L. (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Aphelinus mali (Haldeman) (Hymenoptera: Aphelinidae); Lebanon

Coccinella septempunctata L. (Coleoptera: Coccinellidae); Lebanon, Jordan, Syria

Oenopia conglobata (L.) (Coleoptera:Coccinellidae); Syria, Jordan

Leucoptera scitella Costa (Lepidoptera: Lyonetidae); Algeria[c]

Malacosoma neustria (L.) (Lepidoptera: Lasiocampidae); Libya[c]

Panonychus ulmi (Koch) (Acari: Tetranychidae)

Amblyseius andersoni Chant (Acari: Phytoseiidae); Algeria[c]

Phytoseiulus persimilis Athias-Henriot (Acari: Phytoseiidae); Algeria[c]

Phytoseius plumifer (C. & F.) (Acari: Phytoseiidae); Lebanon

Stethorus gilvifrons (Muslant) (Coleoptera: Coccinellidae); Iraq, Jordan, Lebanon, Syria

Zetzellia mali Oud. (Acari: Stigmaeidae); Lebanon, Syria

Zetzellia talhouki Dosse (Acari: Stigmaiedae); Lebanon

Pterochloroides persicae (Cholod) (Hemiptera: Lachnidae); Lebanon, Syria

Pauesia sp. (Hymenoptera: Aphidiidae); Yemen[c]

Tetranychus urticae Koch (Acari: Tetranychidae)

Amblyseius andersoni (Acari: Phytoseiidae); Algeria[c]

Phytoseiilus persimilis Athias-Henriot (Acari: Phytoseiidae); Algeria[c]

Stethorus gilvifrons (Muslant) (Coccinellidae); Iraq, Jordan, Lebanon, Syria

Zetzellia spp. (Acari: Stigmaeidae); Lebanon, Syria

Tetranychus turkestani Ugarov & Nikolski (Acari: Tetranychidae)

Stethorus gilvifrons (Muslant) (Coccinellidae); Iraq, Jordan, Lebanon, Syria

Tydeus californicus Banks (Acari: Tydeidae); Lebanon[b]

Zeuzera pyrina (L.) (Lepidoptera: Cossidae) Algeria[c], Lebanon, Libya[c], Syria

Peach

Anarsia lineatella Zell. (Lepidoptera: Gelechidae); Palestine, Syria

Aetecerus discolor Wesm. (Hymenoptera: Ichneumonidae); Lebanon

Aulacorthum solani (Kaltenbach) (Hemiptera: Aphididae)

Aphidius matricariae Hal. (Hymenoptera: Aphidiidae); Lebanon, Syria

Bactrocera zonata (Saunders) (Diptera: Tephritidae); Egypt, Middle East[c]

Brachycaudus amygdalinus (Schout.) (Hemiptera: Aphididae)

Episyrphus balteatus (De Geer) (Diptera: Syrphidae); Lebanon, Syria

Brachycaudus helichrysi (Kalt.) (Hemiptera: Aphididae); Iraq, Jordan, Saudi Arabia

Episyrphus balteatus (De Geer) (Diptera: Syrphidae); Lebanon, Syria

Ceratitis capitata Weid. (Diptera: Tephritidae); Egypt, Jordan, Lebanon, Syria[c]

Myzus persicae (Hemiptera: Aphididae)

Praon sp. (Hymenoptera: Aphidiidae); Syria

Syrphus ribessii (L.) (Diptera: Syrphidae); Lebanon, Syria

Trioxys angelicae (Haliday) (Hymenoptera: Aphidiidae); Lebanon, Tunisia[c]

Neurotoma nemoralis L. (Hymenoptera: Pamphiliidae)

Sinophorus (*Limnerium*) *crassifemur* (Thomson) (Hymenoptera: Ichneumonidae); Syria

Pterochloroides persicae (Cholod) (Hemiptera: Lachnidae)
- *Syrphus* sp. (Diptera: Syrphidae); Lebanon, Syria
- *Pauesia antennata* (Mukerji) (Hymenoptera: Braconidae); Yemen

Pear

- *Apiomyia bergenstammi* (Wachtl.) (Diptera: Cecidomyiidae)
- *Oxyglypta rugosa* Rushka (Chalcididae); Lebanon, Syria

Cacopsylla bidens (Sulc.) (Hemiptera: Psyllidae); Lebanon, Syria

Capnodis tenebrionis L. (Coleoptera: Buprestidae); Lebanon

Ceratitis capitata Weid. (Diptera: Tephritidae); Egypt, Jordan[b], Lebanon, Syria[c]

Dysaphis pyri Boy. (Hemiptera: Aphididae); Iraq[b]

Zeuzera pyrina (L.) (Lepidoptera: Cossidae); Algeria[c], Lebanon, Libya[c], Syria

Plum

Acalitus phloeocoptes Nal. (Acari: Eriophyidae)
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Aculus fockeui (Nalepa and Trouessart) (Acari: Eriophyidae)
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]

Bryobia rubrioculus (Scheuten) (Acari: Tetranychidae)
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Cenopalpus lanceolatisetae Attiah (Acari: Tenuipalpidae)
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Diptacus gigantorhynchus (Nalepa) (Acari: Diptilomiopidae)
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Eotetranychus carpini (Oudemams) (Acari: Tetranychidae)
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Hyalopterus pruni (Geoffroy) (Hemiptera: Aphididae)
- *Adonia variegata* (Goeze) (Coleoptera: Coccinellidae); Lebanon, Syria
- *Ephedrus plagiator* (Nees) (Hymenoptera: Braconidae); Lebanon, Iraq[b]
- *Syrphus ribesii* L. (Diptera: Syrphidae); Lebanon, Syria

Phyllocoptes abaenus Keifer (Acari: Eriophyidae)
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Tetranychus cinnabarinus Boisd. (Acari: Tetranychidae); Saudi Arabia, Syria
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Tetranychus urticae Koch (Acari: Tetranychidae); Saudi Arabia, Syria
- *Typhlodromous invectus* Chant (Acari: Phytoseiidae); Lebanon[b]
- *Zetzellia talhouki* Dosse (Acari: Stigmaeidae); Lebanon[b]

Quince

Capnodis tenebrionis L. (Coleoptera: Buprestidae); Algeria

Ceratitis capitata Weid. (Diptera: Tephritidae); Jordan[b]

Recurvaria nanella Hb. (Lepidoptera: Gelechidae); Lebanon
- *Macrocentrus abdominalis* F. (Hymenoptera: Braconidae); Syria
- *Orgilus obscurator* Nees (Hymenoptera: Braconidae); Syria

Strawberry

Phytonemus (*Steneotarsonemus*) *pallidus* (Banks) (Acarina: Tarsonemidae); Lebanon

Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae); Lebanon

Tetranychus urticae Koch
  Phytoseiulus persimilis Athias-Henriot (Acari: Phytoseiidae); Egypt[c], Lebanon

Rutaceae

Citrus

Acaudaleyrodes citri (Priesner & Hosni) (Hemiptera: Aleyrodidae)
  Cales noaki Howard (Hymenoptera: Aphelinidae); Syria[c]
  Encarsia lahorensis (Howard) (Hymenoptera: Aphelinidae); Syria[c]
  Encarsia lutea (Masi) (Hymenoptera: Aphelinidae); Middle East[d]

Acrythosiphon lactucae (Tlja.) (Hemiptera: Aphididae)
  Scymnus apetzi Mulsant (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Aleurothrixus floccosus (Maskell) (Hemiptera: Aleyrodidae)-Syria[c]
  Encarsia lahorensis (Howard) (Hymenoptera: Aphelinidae); Syria[c]

Aonidiella aurantii (Maskell) (Hemiptera: Diaspididae)
  Aphytis chrysomphali (Mercet) (Hymenoptera: Aphelinidae); Lebanon, Syria

Aphis citricola (Van der Goot) (Hemiptera: Aphididae); Syria[c]

Aphis gossypii (Glover) (Hemiptera: Aphididae); Iraq, Jordan, Lebanon, Saudi Arabia, Syria[c]

Aspidiotus hederae Vallot (Hemiptera: Diaspididae)
  Rhizobius lophanthae (Blaisdell) (Coleoptera: Coccinellidae); Jordan, Syria

Bemisia tabaci Genn. (Hemiptera: Aleyrodidae)
  Encarsia lutea (Masi) (Hymenoptera: Aphelinidae); Middle East[d]
  Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]

Brevipalpus lewisi McGregor (Acari: Tetranychidae)
  Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]

Ceratitis capitata Wied. (Diptera: Tephritidae); Jordan, Lebanon, Syria[c]

Ceroplastes floridensis Comostock (Hemiptera: Coccidae)
  Scutellista cyanea Motsch (Hymenoptera: Pteromalidae); Lebanon, Syria[c]

Chrysomphalus ficus Ashm (Hemiptera: Coccidae)
  Aphytis chrysomphali (Mercer) (Hymenoptera: Aphelinidae); Lebanon, Syria

Dialeurodes citri Ashmead (Hemiptera: Aleyrodidae)
  Cales noaki Howard (Hymenoptera: Aphelinidae); Syria[c]
  Encarsia lahorensis (Howard) (Hymenoptera: Aphelinidae); Syria[c]
  Encarsia sp. (Hymenoptera: Aphelinidae); Syria

Diaphorina citri Kuw. (Hemiptera: Psyllidae)
  Chilomenes vicina (Muls.) (Coleoptera: Coccinellidae); Saudi Arabia
  Diaphorencyrtus aligarhensis (Shafee, Alam & Agaral) (Hymenoptera: Encyrtidae); Saudi Arabia

Duraphis noxia (Kurdjumov) (Hemiptera: Aphididae)

Aphidius colemani Viereck (Hymenoptera: Braconidae); Lebanon, Syria
  Aphidius matricariae (Hymenoptera: Braconidae); Lebanon, Syria
  Ephedrus persicae Frogatt (Hymenoptera: Braconidae); Lebanon
  Lysiphlebus fabarum Marshal (Hymenoptera: Braconidae); Lebanon[b]
  Praon volucre (Hymenoptera: Braconidae); Lebanon[b]
  Trioxys angelicae Haliday (Hymenoptera: Braconidae); Lebanon[b]

Eriophyes (*Aceria*) *sheldoni* (Ewing) (Acari: Eriophyidae)
  Phytoseiulus (*Phytoseides*) sp. (Acari: Phytoseiidae); Lebanon, Syria

Eutetranychus orientalis (Klein) (Acari: Tetranychidae)
  Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]
  Exochomus nigromaculatus (Goeze.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Heliothrips haemorrhoidalis Bouche (Thysanoptera: Thripidae)
  Franklinothrips megalops (*myrmecaeformis*) (Thysanoptera: Aeolothripidae); Lebanon, Palestine

Icerya purchasi Mask. (Hemiptera: Margarodidae)
  Rodalia cardinalis (Mulsant) (Coleoptera: Coccinellidae)

Macrosiphum euphorbiae (Thomas) (Hemiptera: Aphididae); Syria[c]

Microtermes najdensis Harris (Isoptera: Termitidae); Saudi Arabia

Nipaecoccus viridis (Newstead) (Hemiptera: Pseudococcidae); Iraq, Jordan, Lebanon, Saudi Arabia

- *Anagyrus* (*Agraensis*) *indicus* Shafee, Alam, & Agarwal (Hymenoptera: Encyrtidae); Jordan, Syria
- *Anagyrus kamali* Moursi (Hymenoptera: Encyrtidae); Jordan
- *Anagyrus pseudococci* Girault (Hymenoptera: Encyrtidae); Saudi Arabia
- *Chrysopa* nr. *gobiensis* (Tjeder) (Neuroptera: Chrysopidae); Saudi Arabia
- *Exochomus marginipennis* Leconte (Coleoptera: Coccinellidae); Saudi Arabia
- *Hyperaspis* sp. (Coleoptera: Coccinellidae); Saudi Arabia
- *Nephus bipunctatus* (includens) Kirsch (Coleoptera: Coccinellidae); Jordan, Syria
- *Scymnus* sp. (Coleoptera: Coccinellidae); Saudi Arabia

Panonychus citri (McGregor) (Acari: Tetranychidae)

- *Amblyseius* (*Iphiseius*) *degenrans* Berlese (Acari: Phytoseiidae); Syria; Lebanon, Saudi Arabia
- *Neoceiulus* (*Amblyseius*) *californicus* McGregor (Acari: Phytoseiidae); Syria
- *Phytoseiulus* (*Phytoseides*) sp. (Acari: Phytoseiidae); Syria

Papilio demodocus (Esper) (Lepidoptera: Papillionidae); Saudi Arabia

Papilio demolus L. (Lepidoptera: Papillionidae); Saudi Arabia

Parabemisia myricae Kowana (Hemiptera: Aleyrodidae)

- *Cales noaki* Howard (Hymenoptera: Aphelinidae); Syria[c]
- *Encarsia lahorensis* (Hymenoptera: Aphelinidae); Syria[c]
- *Eretmocerus* sp. (Hymenoptera: Aphelinidae): Israel[d]

Paraleyrodes minei Iaccarino (Hemiptera: Aleyrodidae)

- *Cales noaki* Howard (Hymenoptera: Aphelinidae); Syria[c]
- *Encarsia lahorensis* (Hymenoptera: Aphelinidae); Syria[c]

Phyllocnistis citrella (Stainton) (Lepidoptera: Gracillariidae); Saudi Arabia

- *Ageniaspis citricola* Logvinovskaya (Hymenoptera: Encyrtidae); Syria
- *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae); Jordan, Syria
- *Cirrospilus ingenus* (Gahan) (Hymenoptera: Eulophidae); Syria
- *Cirrospilus luteus* (Hymenoptera: Eulophidae); Lebanon
- *Cirrospilus lyncus* (Walker) (Hymenoptera: Eulophidae); Lebanon
- *Cirrospilus* nr. *lyncus* (Walker) (Hymenoptera: Eulophidae); Syria
- *Cirrospilus pictus* (Nees) (Hymenoptera: Eulophidae); Jordan
- *Cirrospilus quadristriatus* (Subba Rao & Ramamani) (Hymenoptera: Eulophidae); Jordan, Syria
- *Cirrospilus* sp. (Hymenoptera: Eulophidae); Algeria[c]
- *Citrostichus phyllocnistoides* (Hymenoptera: Eulophidae); Syria
- *Neochrysocharis formosa* (Westwood) (Hymenoptera: Eulophidae); Jordan, Syria
- *Pnigalio* spp. (Boucek) (Hymenoptera: Eulophidae); Algeria[c], Jordan, Lebanon, Syria
- *Ratzeburgiola incompleta* (Boucek) (Hymenoptera: Eulophidae); Jordan, Syria, Saudi Arabia
- *Semielacher petiolatus* (Girault) (Hymenoptera: Eulophidae); Algeria[c], Syria
- *Stenomesius japonicus* (Ashmead) (Hymenoptera: Eulophidae); Syria
- *Sympiesis* spp. (Hymenoptera: Eulophidae); Syria

Phyllocoptruta oleivora (Ashmead) (Acarina: Eriophyidae); Saudi Arabia

- *Phytoseiulus* (*Phytoseides*) sp. (Acari: Phytoseiidae); Lebanon, Syria

Planococcus (*Psuedococcus*) *citri* (Risso) (Hemiptera: Pseudococcidae)

- *Cryptolaemus montruzieri* (Mulsant) (Coleoptera: Coccinellidae), Syria[c]

Planococcus spp. (Hemiptera: Pseudococcidae); Saudi Arabia

- *Anagyrus* (*agraensis*) *indicus* Shafee, Alam, & Agarwal (Hymenoptera: Encyrtidae); Jordan, Syria
- *Pseudococcus adonidum* (L.) (Hemiptera: Pseudococcidae)
- *Cryptolaemus montruzieri* (Mulsant) (Coleoptera: Coccinellidae), Syria[c]
- *Leptomastix dactylopii* Howard (Hymenoptera: Encyrtidae); Syria
- *Nephus bipunctatus* (*includens*) Kirsch (Coleoptera: Coccinellidae); Jordan, Syria

Prays citri Miller (Lepidoptera, Hyponomentidae); Egypt[b]

- *Bracon hebetor* Say. (Hymenoptera: Braconidae); Iraq, Syria
- *Elasmus steffani* (Hymenoptera: Elasmidae); Syria

Scirtothrips citri (Moulton) (Thysanoptera: Thripidae)

Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]

Tetranychus cinnabarinus (Boisd.) (Acari: Tetranychidae)

Exochomus nigromaculatus (Goeze.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Stethorus gilvifrons Muls. (Coleoptera: Coccinellidae); Lebanon

Tetranychus turkestani Ugarov & Nikolski (Acari: Tetranychidae)

Stethorus gilvifrons (Muslant) (Coleoptera: Coccinellidae); Iraq, Jordan, Lebanon, Syria

Chrysoperla carnea Steph. (Neuroptera: Chrysopidae); Iraq

Toxoptera aurantii (Boyer de Fonscolombe) (Hemiptera: Aphididae)

Aphidius colemani Viereck (Hymenoptera: Braconidae); Lebanon, Syria

Aphidius matricariae (Hymenoptera: Braconidae); Lebanon, Syria

Ephedrus persicae Frogatt (Hymenoptera: Braconidae); Lebanon

Lysiphlebus fabarum Marshal (Hymenoptera: Braconidae); Lebanon[b]

Praon volucre; Lebanon[b]

Trioxys angelicae Haliday (Hymenoptera: Braconidae); Lebanon[b]

Solanaceae

Eggplant

Aphis gossypii (Glover) (Hemiptera: Aphididae); Iraq, Jordan, Lebanon, Saudi Arabia

Bemisia tabaci Gen. (Hemiptera: Aleyrodidae); Algeria[c]

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Iraq, Syria[c]

Orius albidipennis Reut. (Hemiptera: Anthocoridae); Iraq[b]

Leucinodes orbonalis Guen. (Lepidoptera: Pyralidae); Egypt, Lebanon, Saudi Arabia

Tetranychus urticae Koch (Acari: Tetranychidae)

Phytoseiulus persimilis (Acari: Phytoseiidae); Lebanon & Syria[b]

Potato

Gnorimoschema (*Phthorimaea*) *operculella* Zeller (Lepidoptera: Gelechiidae); Cyprus, Egypt, Iraq[b] & Jordan, Lebanon, Saudi Arabia, Syria

Chelonus phthoremiaeae Gahan (Hymenoptera: Braconidae); Tunisia

Macrosiphum euphorbiae (Thomas) (Hemiptera: Aphididae); Algeria[c]

Myzus persicae (Sulzer) (Hemiptera: Aphididae); Algeria[c], Lebanon, Saudi Arabia, Syria

Tomato

Aculops (= *Vasates*) *lycopersici* (Massee) (Acari: Eriophyidae); Lebanon, Saudi Arabia

Bemisia tabaci Gennadius (Hemiptera: Aleyrodidae); Egypt[c], Lebanon, Saudi Arabia, Syria, Yemen

Encarsia spp. (Hymenoptera: Aphelinidae); Jordan

Helicoverpa (*Heliothes*) *armigera* Hb. (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia, Syria, Yemen[b]

Liriomyza bryoniae Kalt. (Diptera: Agromyzidae); Iraq[c]

Urticaceae

Figs

Ceratitis capitata Weid. (Diptera: Tephritidae); Jordan, Syria[c]

Ceroplastes rusci L. (Hemiptera: Coccidae)

Ancytus sp.; Syria; Libya[c]

Coccidophaga scitula Ramb. (Lepidoptera); Lebanon

Scutellista cyanea (Motschulsky) (Hymenoptera: Pteromalidae); Jordan, Lebanon, Syria

Tetrastichus sp. (Hymenoptera: Eulophidae); Jordan, Lebanon, Syria

Ephestia cautella (Walker) (Lepidoptera: Pyralididae)

Bracon hebetor Say. (Hymenoptera: Braconidae); Iraq, Syria

Hypoborus ficus Er. (Coleoptera: Scolytidae)

Sycoster lavagnei (Hymenoptera: Braconidae); Lebanon

Rhycaphytoptus ficifoliae K. (Acari: Rhyncaphytoptidae); Iraq[b]

Silba adipata McAlpine (Diptera: Lonchaeidae); Iraq, Lebanon, Turkey

Mulberry

Icerya aegyptiaca Douglas (Hemiptera: Margarodidae)

Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae); Egypt[c]

Euseius scutalis (Acari: Phytoseiidae) (Athias-Henriot); Egypt[c]

Pseudococcus citri Risso (Hemiptera: Pseudococcidae)

Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae); Egypt[c]

Euseius scutalis (Acari: Phytoseiidae) (Athias-Henriot); Egypt[c]

Tetranychus urticae Kock. (Acari: Tetranychidae)

Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae); Egypt[c]

Euseius scutalis (Acari: Phytoseiidae) (Athias-Henriot); Egypt[c]

Vitaceae

Grapes

Colomerus (*Eriophyes*) *vitis* (Pangest) (Acari: Eriophyiidae); Lebanon

Euseius scutalis Athias-Henriot (Acari: Phytoseiidae); Jordan

Lobesia botrana Denis & Schiffermüller (Lepidoptera: Tortricidae); Iran[c], Jordan[c]

Ascogaster quadridentata (Wesmael) (Hymenoptera: Braconidae); Jordan, Syria

Bassus (*Microdus*) *dimidiator* (Nees) (Hymenoptera: Braconidae); Syria

Bracon brevicornis (Wesmael) (Hymenoptera: Braconidae); Syria

Coccinella septempunctata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria

Dibrachys boarmiae (Walker) (Hymenoptera: Pteromalidae); Syria

Pristomerus sp. (Hymenoptera: Ichneumonidae); Syria

Planococcus (*Pseudococcus*) *citri* (Risso) (Hemiptera: Psuedococcidae); Lebanon[b], Syria

Theresimima (*Procris*) *ampelophaga* B.-B. (Lepidoptera: Zygaenidae); Jordan, Lebanon, Syria

Viteus vitifolii (Fitch.) (Hemiptera: Phylloxeridae); Jordan, Lebanon, Syria

Miscellaneous

Stone fruit trees

Capnodis tenebrionis L. (Coleoptera: Buprestidae); Jordan[c], Lebanon, Syria

Capnodis carbonaria Klug. (Coleoptera: Buprestidae); Jordan[c], Lebanon, Syria

Storage pests

Beans (Leguminosaea)

Bruchus dentipes Baudi (Coleoptera: Bruchidae)

Triaspis thoracicus (Curtis) (Hymenoptera: Braconidae); Syria

Callosobruchus chinensis L. (Coleoptera: Bruchidae); Syria[b]

Chickpeas (Leguminosaea)

Bruchus dentipes Baudi (Coloeptera: Bruchidae); Syria[b]

Callosobruchus chinensis L. (Coloeptera: Bruchidae); Syria[b]

Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Cotton (Malvaceae)

Tribolium castaneum (Herbst) (Coleoptera: Tenebrionidae)

Trichogramma principium (Hymenoptera: Trichogrammatidae); Iraq[b]

Cowpeas (Leguminosaea)

Collosobruchus maculatus F. (Coleoptera: Bruchidae); Iraq[b], Syria

Lentils (Leguminosaea)

Bruchus dentipes Baudi (Coleoptera: Bruchidae); Syria[b]

Callosobruchus chinensis L. (Coleoptera: Bruchidae); Syria[b]

Sesame (Pedaliaceae)

*Trog*oderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Sunflower (Asteraceae/Compositae)

Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Wheat (Gramineae/Poaceae)

Sitotroga cereallella (Olivier) (Lepidoptera: Gelechiidae); Iraq

Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Vegetables

Agrotis ipsilon (Rottemburg) (Lepidoptera: Noctuidae); Lebanon, Saudi Arabia, Syria

Apanteles ruficrus Hal. (Hymenoptera: Braconidae); Egypt

Earias biplaga Walker (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia, Syria

Empoasca lybica De Bergevin (Hemiptera: Cicadellidae); Egyptb, Lebanon, Saudi Arabia, Sudan, Syria

Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae); Egypt[b]

Spodoptera exigua (Hb.) (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia, Syria

Trichoplusiani (Hübner) (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia

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Pest Species

Any species that humans consider to be undesirable. More often, a pest is considered to be a species that competes with humans for food, fiber, or shelter, or transmits diseases to humans or livestock, or affects the comfort of humans.

Petaluridae

A family of dragonflies (order Odonata). They commonly are known as graybacks.

► Dragonflies and Damselflies

Petiolate

Attached by a narrow stem or stalk (a petiole).

Petiole

Stalk that connects the leaf to a stem. In Hymenoptera, it is sometimes used to describe the first section of the narrow stalk-like abdominal segment, or "waist."

► Abdomen of Hexapods

Petrunkevitch, Alexander

Alexander Petrunkevitch was born at Pliski, Russia, in December 1875. He was born into a noble family, and at an early age displayed interest in both zoology and the literary arts. His liberal politics forced him to leave Russia, and he moved to Germany, where he came under the influence of August Weismann. He completed a Ph.D. dissertation in 1900 on the cytology and embryonic development of the honey bee, and married an American. They moved to the United States in 1903, and he became a lecturer at Harvard University in Boston, and then acting professor of Zoology at Indiana University, though he commuted regularly to Massachusetts to be with his wife, who had become ill. He moved to Yale University when his wife contracted tuberculosis, becoming an assistant professor in 1911 and a full professor in 1917. Petrunkevitch made important contributions to the study of arachnids. Among his important publications were "A synomic index-catalogue of spiders of North, Central and South America" (1911)," "On families of spiders" (1923), "Catalog of American spiders-part I" (1939), and "An inquiry into the natural classification of spiders, based on a study of their internal anatomy" (1933). He died in New Haven, Connecticut, on March 9, 1964.

Reference

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Phacopteronidae

A family of bugs (order Hemiptera, superfamily Psylloidea).

► Bugs

Phage (Bacteriophage)

A virus that attacks bacteria. Frequently used as vectors for carrying foreign DNA into cells by genetic engineers.

Phalacridae

A family of beetles (order Coleoptera). They commonly are known as shining flower beetles.

► Beetles

Phagocytes

Cells that are capable of moving in the insect body and engulfing or destroying small foreign bodies such as microorganisms.

Phagostimulant

A substance that induces feeding.

Phagocytosis

The process of ingestion and digestion by cells, especially the ingestion or engulfing of microorganisms and other small particles by blood cells.

Phallus

The intromittent (copulatory) organ of insects; the aedeagus and any processes found at its base.

Phantom Crane Flies

Members of the family Ptychopteridae (order Diptera).

► Flies

Phantom Midges

Members of the family Chaoboridae (order Diptera).

► Flies

Pharate

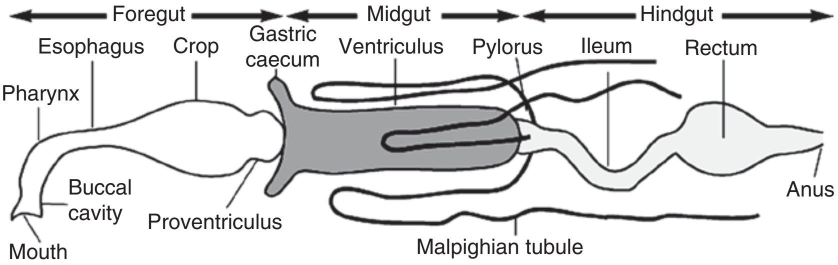
The stage at which molting has started but the insect has not yet cast off the old cuticle.

Pharynx

The anterior portion of the foregut immediately behind the buccal cavity (Fig. 31).

► Alimentary System

► Alimentary Canal and Digestion



Pharynx, Figure 31 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

Phase Polymorphism in Locusts

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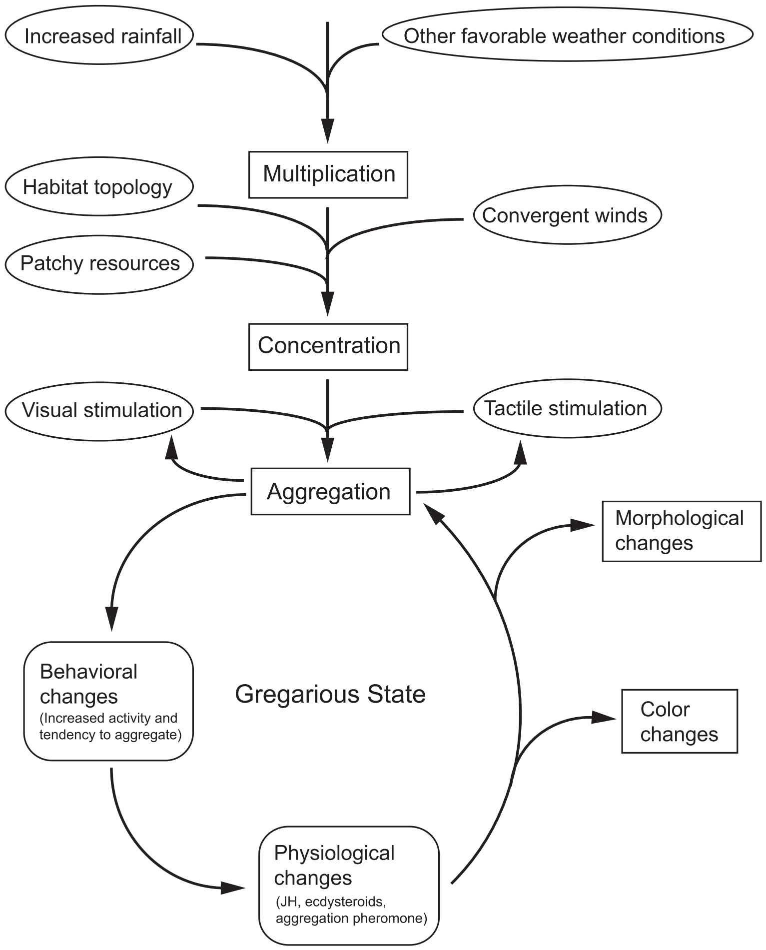
Insects regularly encounter large fluctuations in environmental conditions to which they must adapt in order to survive. Some of these conditions include temperature change, photoperiod, host plant quality and availability, and conspecific and heterospecific species density. These conditions can change rapidly and, in order to survive, insects must adapt to them within a single or only a few generations. One way insects can accomplish this is through a physiological change such as polymorphism. Polymorphism is the presence of multiple phenotypes of organisms in the same species, accomplished through differential gene expression. Polymorphism can affect several aspects of an insect's biology such as behavior, appearance, reproductive capability, or dispersal ability. This is often accomplished through a complex series of events, which at the most basic level involves differences in gene transcription and translation. Polymorphisms occur across the animal kingdom and, of course, in Insecta. Polymorphism affecting dispersal capability, often called dispersal phase polymorphism, occurs in Psocoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera. The variety of polymorphisms, and the broad range of taxa in which polymorphisms occur, implies that there must be some benefit in possessing the ability to change in response to environmental conditions.

Dispersal Polymorphism

Dispersal polymorphisms have been widely studied, and the knowledge gained has led to some insights into why a mechanism like polymorphism would evolve. A change such as an insect's ability to disperse should be related to large-scale changes in the environment that would necessitate dispersal to a new one. Therefore, dispersal should be essential in temporary habitats, but minimized in persistent habitats. However, this does not always hold true. Other factors such as crowding, host plant condition, temperature, and photoperiod have been shown to influence dispersal capability. These factors may either initiate or intensify the process.

Dispersal polymorphism is most easily recognized in insects as differences in wing size, but can also be expressed as differences in flight muscle mass, behavior, and storage and metabolism of energy reserves. Migration from an unsuitable habitat to a more suitable one requires relatively greater energy reserves. Many species exhibiting wing polymorphism have their flight capability negatively correlated with age at first reproduction and fecundity. Insects that show this negative correlation in having their macropterous forms less fecund than their brachypterous forms include grasshoppers, crickets (both Orthoptera), planthoppers, aphids, waterstriders, veliids, water boatmen, seed bugs (all Hemiptera), and pea weevils (Coleoptera). Other costs of being macropterous include decreased longevity, and reduced egg or offspring size. Negative correlations between dispersal ability and reproduction have led to the notion that there is a trade-off between flight capability and reproduction, two very energetically expensive processes. General maintenance costs in herbivorous insects can comprise up to thirty percent of their total energy budget. With such a large amount of resources being dedicated to maintenance, reducing the amount of tissue having to be maintained would be an easy way to save resources. In brachypterous forms, this is exactly what happens. Reduction of wing size and flight muscle mass saves energy in the production of these tissues and reduces the overall costs of maintenance in the insect. Reduction of tissues can occur during development or after development, by breaking down already-present tissues. Histolysis of flight muscle in the Colorado potato beetle, *Leptinotarsa decemlineata*, before it overwinters is thought to conserve energy. Flight muscle proteins are adsorbed by growing oocytes in *Dysdercus cingulatus* bugs. This example provides evidence that energy saved from reducing flight muscle mass can be used directly in the production of oocytes, and that a trade-off between dispersal ability and reproduction is possible. In terms of evolution, it would make sense that those insects not needing to disperse or migrate should not waste energy on producing and maintaining expensive flight muscles. However, there is another aspect that must be considered, and that is the timing of phase determination, or the time an individual becomes committed to a particular phase. In general, there are two modes of phase determination timing, early and late. Each of these modes has particular evolutionary advantages and disadvantages. Early-stage determination allows maximum commitment of resources and more efficient morphs. This can be beneficial in environments that change slowly over time, but when environmental changes occur rapidly it would be more advantageous to be able to adapt quickly. Late-stage development allows this adaptation to sudden changes in conditions.

There are many reasons why it might have been advantageous for polymorphism to have evolved. In fact, the diversity of taxa possessing polymorphism, and variety of mechanisms and stimuli involved, suggest it has evolved independently many times throughout Insecta. One group of insects in which development of polymorphism has been advantageous for is the orthopteran family Acrididae, particularly the locusts. Locust phases exhibit marked differences in behavior, physiology, biochemistry, morphology, and pigmentation. These differences were so dissimilar that locusts exhibiting them were thought to be different species. Boris A. Uvarov realized that the different phases were actually the same species and coined the term phase polymorphism for referring to the shifts in phase occurring in locusts (Fig. 32).



Phase Polymorphism in Locusts, Figure 32 **Major component processes of phase transformation in locusts.**

Environmental Factors Inducing Phase Differentiation in Locusts

Phase determination in locusts is largely based on the degree of crowding or density of the locusts, and the length of time to which they are exposed to this density. Increases in favorable weather conditions such as rainfall and food quality can cause a general increase in abundance of individuals. With increased population numbers, crowding of individuals is more likely, and can be promoted by such things as convergent winds, habitat topologies, and patchy distributions in harborages, food distribution, and oviposition sites. As crowding occurs due to these factors, behavior is altered to promote further crowding. This causes a positive feedback loop that, in combination with continued favorable environmental conditions, pushes the population further towards the gregarious phase.

Differences Between Phase States: Solitarious Versus Gregarious

Phase polymorphisms often exhibit a continuum of states with two extremes, one being the solitarious state and the other the gregarious state (Table 11). The intermediate state is sometimes called "transiens." In populations with low densities, individuals are in the solitarious state and are relatively inactive, exhibit cryptic coloration, and are widely dispersed, avoiding one

Phase Polymorphism in Locusts, Table 11 Some differences between locust phases

	Solitarious	Gregarious
Behavior		
Tendency to aggregation	Absent	Present
Aggressive toward conspecifics	Yes	No
Activity level	Lower	Higher
Activity rhythm	Not synchronized	Synchronized
Adult flight	Nocturnal	Diurnal
Physiology		
Hemolymph polypeptides	3 specific	17 specific
Juvenile hormone levels	Higher	Lower
Nymphal ecdysteroid levels	Lower	Higher
Adult ecdysteroid levels	Higher	Lower
Lipid reserves	Lower	Higher
Carbohydrate level	Lower	Higher
Respiratory rate	Slower	Faster
Adipokenetic reaction	Lower	Higher
Glycolytic enzyme levels	Lower	Higher
Early mortality of young	Higher	Lower
Extra larval molt	Yes	No
Nymphal development rate	Slower	Faster
Adult sexual maturation rate	Faster	Slower
Fecundity	More, smaller eggs	Fewer, larger eggs
Life span	Longer	Shorter
Nymphal coloration	Cryptic/Uniform	Dark patterns on light background
Adult coloration	No change	Changes with sexual maturation
Morphology		
Overall size	Larger	Smaller
Head	Smaller	Larger
Tegmen	Shorter	Longer
Hind femur	Longer	Shorter
Sexual-size dimorphism	Pronounced	Slight

another. In populations with high densities, individuals are in the gregarious state and are relatively active, exhibit dark coloration and markings (depending on the species), and are crowded on patchy resources where they tend to aggregate.

Developmental and Reproductive Differences

Solitarious and gregarious locusts exhibit differences in several characters, two of these being developmental rate and fecundity. For example, *Schistocerca* *gregaria* (Orthoptera: Acrididae), when reared under isolated conditions, undergoes an extra larval molt. The incidence of the extra larval molt increases with the duration of isolated development. In the grasshopper *Humbe tenuicornis* (Orthoptera: Acrididae), laboratory reared, adult isolated females are significantly larger and live longer. In general, adult solitarious females of grasshoppers and locusts mature more rapidly and deposit more eggs than do adults from crowded culture. The onset of egg production begins 5 days earlier in solitarious *S. gregaria* than in gregarious forms. Solitarious females of *S. gregaria* produce a greater number of eggs per pod than gregarious females, and have an increased number of ovarioles and a decrease in the number of nonfunctional oocytes.

Metabolic Differences

Another way in which the phase states of locusts differ is in the amount of metabolically derived storage compounds present, and the ability to convert these compounds to energy. Nymphs of solitarious *S. gregaria*, when compared to gregarious individuals, show low carbohydrate levels in the hemolymph and a reduced respiratory rate as evidence of a reduced metabolism. In nymphs of *Locusta migratoria* (Orthoptera: Acrididae) and *Aiolopus thalassinus* (Orthoptera: Acrididae) reared at high population density, CO_2 release is significantly higher than those reared in solitude. Gregarious nymphs and adults of *L. migratoria* show increased lipid levels in their hemolymph when compared to solitarious individuals. In *S. gregaria*, newly emerged solitarious females have relatively smaller fat bodies and less absolute triacylglycerol reserves. Lipid storage is an important factor in an insect's ability to migrate long distances, and phase specific differences in lipid content of the hemolymph may be partly responsible for differences in dispersal ability of the phases. Locusts can also differ in their ability to utilize ingested and stored nutrients, which could also affect dispersal ability. The adipokenetic reaction, which is responsible for the mobilization of lipids, can be induced by a 60 min flight in the laboratory. The reaction is distinctly higher in gregarious females than in solitarious females of *S. gregaria*. In *L. migratoria*, glycolytic enzymes are expressed at different levels in solitarious and gregarious forms. Different isoenzymes of aldose appear at high and low densities, and 2-glycerol-3-phosphate dehydrogenase isoenzymes (enzymes that break down compounds important in lipid metabolism) are higher in low-density larvae. Physiological changes such as these tend to change rapidly in response to changes in density. Such evidence provides more support for the idea that gregarious locusts are better equipped for migratory flights. Paired with the fact that fecundity is reduced, it provides additional evidence for a trade-off between flight capability and reproduction.

Morphological Differences

Phase differences in physical characteristics such as tegmen and femur length are very common in locusts, and are often used in studies to define the phase state of an individual. However, morphometrics should not be used in studies where immediate changes must be recorded, for it may take several generations to see the full effect of treatment on morphometric measurements. For example, in a recent study, two natural subpopulations were brought into laboratory, reared, and phase state determined. The gregarious subpopulation was reared under crowded conditions, while the solitarious subpopulation was reared in isolation. The F/C (femur/width of head between the eyes) ratios of both the original populations were within the solitarious range. But, after two laboratory generations, the F/C ratios of gregarious females had more gregarious F/C ratios than when compared to their parents, or to the solitarious population. What advantages such changes might provide are uncertain, but in locusts it seems to enhance dispersal ability. Locust phases have also been shown to differ in the selectivity and abundance of antennal sensilla. It is thought that such differences might influence density dependent responses by changing the way an individual perceives certain stimuli.

Chromatic Differences

Some of the most obvious characters by which gregarious and solitarious individuals differ are differences in background color, and presence and intensity of dark markings on the body. In locusts, cryptic coloration is generally found in low density populations. Solitarious nymphs of *L. migratoria* show various body colors, depending on habitat, some of these include green, brown, red, and black. In *S. gregaria*, solitarious nymphs are green for the most part, while gregarious nymphs are noticeably melanized. In both of the aforementioned species, gregarious nymphs become more similar to each other in coloration, with distinct black patterns on an orange background. For locusts which tend to bask, darkened cuticle could improve absorption of solar radiation adsorption and cause an increase in nymphal development rate. Such darkening of the cuticle could have been a mechanism evolved to offset the reduced development rates and reproduction exhibited by many gregarious locusts. Research up to this point has shown there to be several compounds responsible for controlling the pigmentation between different phases in locusts. Some of these include juvenile hormone and [His7]-corazonin.

Behavioral Differences

While the changes in color and morphology are easily quantified and evaluated, they may take several generations to manifest themselves. Moreover, they do not necessarily occur in all locusts. A variant population of *L. migratoria* in Israel shows no morphometric or chromatic responses to density. It does, however, show a behavioral response. Behavioral changes are imposed rapidly and are one of first characters to vary in response to density changes. This makes behavioral differences relatively useful in studies, where they can help separate gregarious from solitarious states. The disadvantage of using behavioral differences to determine phase state is that they are hard to quantify and measure accurately, and the measurements taken can be subjective. Another factor that may hinder quantifying behavior is that relative intensity of behavioral responses depends on the degree and duration of crowding experienced by the insect, and by previous generations, and that behavior tends to be the most labile component in phase transition.

Many different aspects of behavior vary between gregarious and solitarious individuals, such as aggregation, general activity level, mating, and oviposition, with aggregation being the most prominent and well studied. Locusts in the gregarious phase show a propensity to aggregate and form bands or swarms. Crowded insects are generally more active and orient towards other individuals, which may lead to behaviors associated with aggregation, such as marching and swarming. The exact opposite occurs in solitarious locusts, which tend to avoid one another and even show aggressive behavior toward each other. Reproductive behaviors such as mating and oviposition are also phase dependent. For male locusts under crowded conditions, mate-finding is not an issue, and sperm competition becomes their main dilemma, which increases mate guarding behavior. Female *S. gregaria* locusts under crowded conditions deposit eggs at common sites, and this aggregated oviposition may be pheromone mediated.

Stimuli Inducing or Enhancing Phase State

The induction of a phase state involves a series of steps. The first is stimuli that induce the phase change. The second is the physiological processes that are initiated by these stimuli. The third is the visible change or difference that occurs between phases. Following are four types of stimuli that occur in a group of locusts that induce or enhance phase state in locusts: visual, auditory, chemical, and tactile.

Tactile Stimuli

Tactile stimulation seems to be the most potent stimulus inducing the gregarious state, with all other stimuli further enhancing its effect. Even tactile stimulation with paper maché balls or millet seeds can induce a phase change. This is not to say that only tactile stimulation induces the gregarious phase. Many stimuli can initiate a phase change when in combination with each other, while a few can initiate a weak response. Nymphs of *S. gregaria*, when reared in contact with other locusts (either conspecific or heterospecific), develop black markings. However, full development of the yellow background color in final instar nymphs only occurs when nymphs are reared with conspecifics. Visual and chemical stimuli can cause black coloration, but black coloration is not enhanced by the addition of tactile stimulation. Tactile stimulation inducing gregarious characteristics is particularly effective on the hind femora in *S. gregaria*, where both exteroceptive and proprioceptive mechanosensory components were found to be involved, traveling through leg nerves. Tactile stimulation is a key component in the positive feed-back loop that drives a population towards being more gregarious. As locusts get closer, physical contact induces a behavioral change which brings them even closer together increasing the stimulus which further alters their behavior to the gregarious state.

Visual Stimuli

Visual stimuli play an important role in attraction in gregarious locusts and repulsion in solitary locusts over short distances. By influencing the density of locusts, by either attraction or repulsion, visual stimuli can indirectly affect phase state. However, there is some evidence that visual stimuli are important in determination of phase state. In *S. gregaria*, visual and olfactory stimuli are weakly stimulating when presented alone, unless the period of exposure is greater than 24 h, in which case visual stimuli are moderately stimulating. But, when presented together, they have marked effects on behavior, causing individuals to become more gregarious. In nymphs of *S. gregaria*, olfactory contact with gregarious conspecific or heterospecific locusts fails to induce a behavioral change, but, when presented with visual and olfactory stimuli, behavioral gregarization occurs. This clearly shows that visual and olfactory stimuli are necessary for shifting phase states in the absence of tactile stimuli.

Chemical Stimuli: Olfactory and Contact Chemicals

In general, there are two types of chemical signals an insect can perceive, those produced by volatile chemicals and those produced by contact chemicals. The roles that chemical signals play in phase determination in locusts have been strongly debated, and the debate has been fueled by conflicting evidence from different studies.

One chemical that is currently under debate is phenylacetonitrile. Gregarious males of *S. gregaria*, when becoming sexually mature, release large amounts of a blend of chemicals thought to be active as an aggregation pheromone. Phenylacetonitrile was originally described as the main component of this aggregation pheromone blend, which also contains low amounts of phenol, guaiacol, and benzaldehyde. This aggregation pheromone supposedly can cause locusts to aggregate and perhaps play an important role in arrestment and recruitment of solitary individuals into gregarious groups.

However, in some studies phenylacetonitrile has no attractiveness to fifth instars, or young or mature adults of either sex, suggesting that phenylacetonitrile is not involved in aggregation. An alternative hypothesis as to the function of phenylacetonitrile is that it may function in reproductive behavior under crowded conditions, because of its association with male maturation and increased competition. It has been reported that phenylacetonitrile is released only if other mature males are present, and the amount released depends on the number of males present. Phenylacetonitrile may also act as an anti-aphrodisiac by "hiding" the female and preventing other males from attempting to mount the guarded female, enhancing their mate guarding ability. It also prevents homosexual encounters, which could occur often under crowded conditions. However, it is possible that phenylacetonitrile can affect both aggregation and reproductive behavior, and that the response is somehow dependent on age and level of juvenile hormone. Regardless of its function, changes in emission of aggregation pheromone by adult desert locusts occur rapidly in response to shifts from crowded to solitary rearing conditions, and vice versa. Aggregation pheromone production is so sensitive to density change that there is greater production at a density of four than at two, and it is because of this sensitivity that some have suggested pheromone production be used as a way to measure phase change.

Non-volatile contact chemicals may also play a role in phase determination. Cuticular hydrocarbons have a gregarizing effect on behavior in adult *S. gregaria*, though exposure to cuticular hydrocarbons, either as a single treatment or in combination with mechanical or visual treatments, does not elicit any measurable behavioral gregarization in fifth instars of *S. gregaria*. In another study, locust odor caused an attraction to stimulus source but did not have a gregarizing effect, while chemotactile stimuli had a gregarizing effect but was not attractive to locusts. While the action of cuticular hydrocarbons is debatable, one thing is for sure, and that is cuticular hydrocarbons of gregarious *L. migratoria* and S. *gregaria* differ considerably, as full development of the yellow background color in the last instar of *S. gregaria* nymphs only develops when they are in contact with conspecifics. This implies the presence of species-specific chemical cues or contact pheromones.

Some Physiological Mechanisms Behind Phase Polymorphism

At the core of all the different characteristics that separate gregarious and solitarious locust, and the stimuli which induce these differences, are the physiological and biochemical reactions that occur within the organism. In *S. gregaria*, 17 polypeptides are specific to the gregarious phase and three are specific to the solitarious phase. The presence and quantity of these polypeptides are affected by rearing density and juvenile hormone. This is clear evidence that the different phases of locusts exhibit differences in gene transcription and/or translation. Differences in physiology between gregarious and solitarious phases include hemolymph polypeptides, the density dependent yellow protein, neurotransmitters, juvenile hormone, ecdysteroids, neuropeptides such as corazonin, neuroparsins, and insulin, pheromones such as phenylacetonitrile, and protease inhibitors. Hormones have been especially well investigated.

Juvenile Hormone (JH) and its Analogues

The function of JH has been researched extensively in insects, and its function in phase polymorphism is no exception. JH has been shown to affect several aspects of the differences between phase states. When gregarious male locusts are treated with JH, nine of the 17 gregarious-specific polypeptides are no longer expressed, and two of the three solitarious-specific polypeptides are newly expressed. Thus, JH appears to have a solitarizing effect. Cryptic coloration that is associated with the solitary phase, such as green, is induced by the application of JH in *L. migratoria*, *S. gregaria*, and *S. americana*. JH and its analogues have been shown to have a solitarizing effect on the maximum weight and weight gain in *S. gregaria*. Application of JHIII to gregarious females increases weight gain to maximum weight by 4 days. BASF 228743 (a JH analogue) shows a stronger effect than JHIII, and allows gregarious females to attain a higher maximum weight than solitarious females. JH analogues, and not so much JHIII, reduce aggregation in *S. gregaria* and *L. migratoria* larvae, again a solitarizing effect.

JH and JH analogues have also been shown to take part in the energetic trade-off between flight capability and reproduction. Most of the evidence for this has come from studies on *S. gregaria*. Treatment of gregarious females with JH or JH analogous reduces fat body content levels to levels characteristic of solitarious females. The application of JH also suppresses the adipokenetic reaction in gregarious females as compared to gregarious control females. The appearance of vitellogenin in hemolymph occurs at 7 days for solitarious females, and at 12 days for gregarious females. Application of JH or JH analogous causes gregarious time periods to be more like solitarious ones. Treatment with JH or JH analogous causes an early onset of oocyte development in gregarious females as compared to untreated gregarious females. JH seems to be in control of two very important mechanisms that regulate a trade-off between energy storage for flight, and energy utilization for reproduction. The effects of JH on these processes also seem to be solitarizing, and it may be safe to say that, in general, JH is responsible for several characteristics exhibited by the solitarious phase.

Ecdysteroids

Originally, ecdysone was identified as an insect molting hormone, but ecdysone also occurs in adults in which no molting occurs. Therefore, there must be some other purpose for ecdysone to be present. It is known that prothoracic glands in locusts persist into adult at least until sexual maturation occurs. However, they do not release any significant amount of ecdysteroids in male or female, solitarious or gregarious adult *S. gregaria*. The removal of prothoracic glands from adult *L. migratoria* does not affect the titre of ecdysteroids in the hemolymph. Therefore, ecdysteroids must be originating from some other tissue. Indeed, ecdysteroids are found to be present in eggs and the ecdysteroids originate from the ovaries, which can release the chemical into the hemolymph in some species.

One important function of ecdysteroids could be the control of vitellogenin production, which was documented in *L. migratoria*. The same may be true for *S. gregaria*. Ecdysteroid titres of adult solitarious *S. gregaria* are much higher than in gregarious adults. Maximum levels of hemolymph ecdysteroids in gregarious females are about 150 ng of 20-hydroxyecdysone/ml, as compared to 400 ng of 20-hydroxyecdysone/ml found in solitarious females. There are two peaks in the ecdysteroid titre in *S. gregaria* males and females. In females, the first peak occurs with the first release of vitellogenin synthesis, while the second is timed with egg chorionation. In males, the first peak may control spermatogenesis and accessory gland function, while the second peak coincides with production of pheromones involved in aggregation and maturation. Thus, ecdysteroids are intimately involved in sexual maturation and perhaps interact with JH.

Corazonin

Corazonin is a neurohormone often associated with the corpus cardiacum, and it and similar compounds occur in many arthropods including crustaceans. In insects, it most commonly occurs as one of two forms, [His7]-corazonin or [Arg7]-corazonin. [His7]-corazonin was first discovered in *S. americana*. At the time of discovery, however, its function was unknown. [Arg7]-corazonin, a variant of corazonin that differs by a single amino acid (arginine instead of histine) was first isolated from the corpus cardiacum of the American cockroach, *Periplaneta americana*, as a potent cardiostimulatory peptide. Later studies showed that neither form of corazonin had cariostimulatory effects on *S. americana*, leaving its function in locusts unknown. Subsequent studies have shown that corazonin affects dark pigmentation in locusts. The albinism in the well known Okinawa strain of

L. migratoria is caused by a deficiency of peptides present in the central nervous system, one of these being corazonin. Implantation of a brain or corpus cardiacum taken from normal individuals, *S. gregaria*, other acridids, cockroaches, katydids, crickets, and moths, or injection of methanolic extract, induces dark color in albinos. Injection of [His7]-corazonin, at doses as low as 10 fmol (femtomole, 10^{-15}), induces dark coloration in nymphs of both *L. migratoria* and *S. gregaria*. The response to corazonin is dose dependent, and the higher the dose the darker the color, with very high doses turning most species completely black. Timing of injection is also important. As time of injection is delayed individuals become less black and develop lighter color backgrounds with dark markings. Therefore, both the amount and timing of corazonin present are important in causing the dark coloration exhibited by many gregarious locusts. Corazonin may also have gregarizing effects on behavior and morphological characters such as the number of antennal sensilla.

Proliferation of the Gregarious State

Changes in a locust's phase are not only influenced by the individual's crowding experience, but also by its parents' exposure. This may help explain why locust plagues can persist for several years. Boris A. Uvarov was one of the first scientists to mention that the parental experience of crowding may be transmitted to the next generation of locusts. Some of the first evidence for this was the discovery of behaviorally active compounds that elicit aggregated oviposition are found in the froth of egg pods and include acetophenone and veratrole. Additionally, straight chain unsaturated ketones occur in the sand around oviposition sites and may increase the aggregation response. However, the color and gregarious state of hatchlings is not directly related to the density of egg pods in the area, but is more heavily influenced by the crowding experienced by the adult females. Perhaps the crowding of egg pods is a way of promoting gregarization after hatch by increasing the density of hatchlings in a particular area. It may be possible that these compounds have multiple functions, acting as an attractant for oviposition and as a gregarizing factor for newly hatched nymphs. In response to crowding, accessory glands produce water soluble compounds that can be found in the egg foam that result in the gregarization of developing hatchlings. These compounds were shown to be effective only if present in the first few hours after oviposition. It is unclear if the aforementioned compounds are identical to the oviposition aggregation compounds mentioned earlier.

Compounds found in the egg foam are not the only chemicals responsible for the gregarization of newly hatched nymphs. The hatchlings of gregarious females contain five times more ecdysteroids than those of solitarious females. Eggs of gregarious and solitarious females contain similar ratios of ecdysteroids, but occur at significantly higher levels in the eggs of gregarious females. Eggs from solitary females that experience crowding soon before oviposition show no increase in the amount of ecdysteroid present, suggesting the necessity for a prolonged exposure to crowding. Over incubation time, the change in levels of ecdysteroid content of eggs from gregarious females does not follow the same pattern as levels in eggs from solitarious females. Solitary eggs show a continuous increase in the levels of ecdysteroids, while gregarious eggs show two peaks followed by a decline in ecdysteroid content. This may help explain why adult solitarious locusts have high levels of ecdysteroids while gregarious locusts have low levels. The role of ecdysteroids in the proliferation of the gregarious state is not yet completely understood and it is unclear why ecdysteroid level would differ from egg and nymphal stage to adulthood. What is certain is that the transition to and subsequent retention and proliferation of the gregarious state contains a multitude of interactions that should be further studied.

► Polyphenism in Insects and Juvenile Hormone (JH)
► Corazonin

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Phasic Receptors

Sensory neurons that adapt rapidly to continuing steady stimuli, with the receptor potential falling, and the neuron becoming relatively insensitive. (contrast with tonic receptors).

Phasmatidae

A family of walkingsticks (order Phasmatodea). They commonly are known as winged walkingsticks.

► Walkingsticks and Leaf Insects

Phasmatodea

An order of insects. They commonly are known as walkingsticks and leaf insects.

► Walkingsticks and Leaf Insects

Phenacoleachiidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Phengodidae

A family of beetles (order Coleoptera). They commonly are known as glowworms.

► Beetles

Phenogram

A branching diagram that links different taxa by estimating overall similarity based on data from characters. Characters are not evaluated as to whether they are primitive or derived.

Phenological Asynchrony

Lack of simultaneous occurrence between an insect and its host, or lack of correspondence between traits of organisms (contrast with phenological synchrony).

Phenological Synchrony

Seasonal correspondence between an insect and its host, or seasonal correspondence between traits of organisms (contrast with phenological asynchrony).

Phenology

The seasonal life history of a plant or animal, especially in relation to weather and climate.

Phenology Models for Pest Management

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All living organisms use various "substances" for their energy, body growth, and tissue maintenance.

Enzymes control the use of those substances. Enzymes are very large, complex protein molecules that are formed within cells.

Enzymes have very important roles to play within the life of an organism. In the most general terms, they function to increase the rate of various chemical reactions (catalysts). In more specific terms, they are involved in the removal of electrons from some chemical compounds, the transfer of chemical groups from some compounds to others, the "breaking apart" of larger molecules (digestion), and the linking together of some molecules. Their function within an organism is affected by several factors, one of which is temperature.

For those reactions in which enzymes are involved, there is a range of temperatures within which they will take place. For temperatures that are less than the least value in that range, no reactions will occur. For temperatures that are greater than the greatest value in that range, the enzyme is denatured and coagulates, so no reactions will occur. For temperatures within that range, the rate of reactions increases with increasing temperatures.

The most general measure of enzymatic activity within an organism is, of course, "growth." Growth can be measured in many ways, two of which are the length or height of an organism, and its weight. The growth of an insect to certain discrete stages, such as the larval, pupal, or adult stages, is often referred to as "development." When development is linked with temperature, it is referred to as "phenology."

Growth and development of some organisms, such as humans, may be independent of the temperature that is outside their bodies because their body temperature is fairly constant and always warm. Such organisms are called "homoiotherms." Due to their relatively constant cellular temperatures, the growth of homoiotherms proceeds at a constant rate which can be predicted by "calendar time" (i.e., days, weeks, months, years).

In contrast, development of some other organisms, such as insects, cannot be predicted using calendar time because their body temperature is not maintained at a constant, warm level. Rather, their body temperature largely fluctuates with environmental temperatures. Such organisms are called "poikilotherms." As the cellular temperatures of poikilotherms are not constant, and the level of enzymatic activity is linked with environmental temperatures, their growth and development can usually be predicted through "thermal time."

Thermal time is calculated by first determining the amount of heat that is experienced during a 24 h period. That heat can be expressed as units of heat, or "heat units," also known as degree-days, day-degrees, and thermal units (more on that later). Thermal units are daily amounts of the total heat needed for a poikilotherm to develop to a given growth stage. The total heat needed before a poikilotherm will grow to that stage is sometimes called the effective cumulative temperature, required degree-days, or required thermal summation.

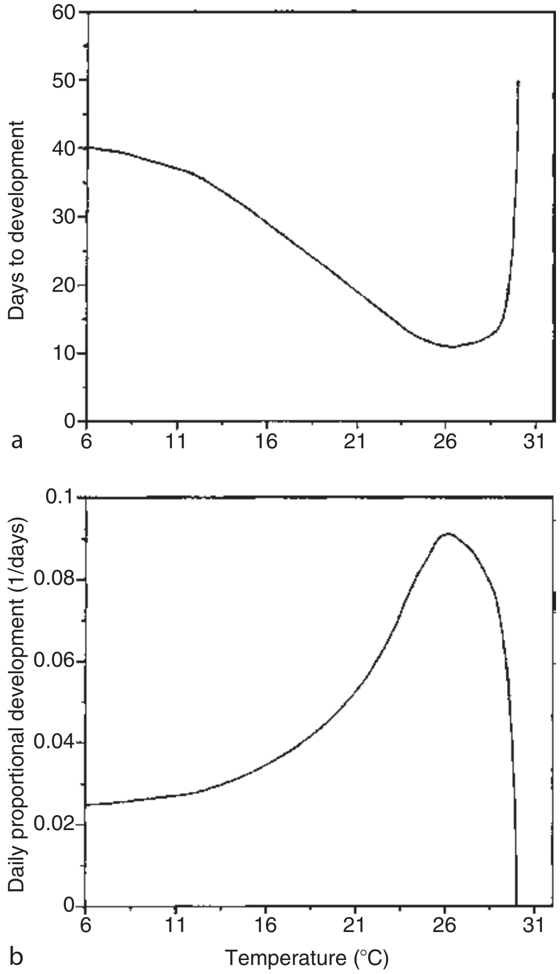
Thermal time can be used to predict the growth of an individual insect by having pest managers calculate and sum thermal units, from one 24-h period to another, until that sum equals the required thermal summation; the date on which that occurs is, theoretically, the date on which the growth of that insect has reached a specific stage. Pest managers often wish to predict insect developmental events, such as egg hatch, which can signal the onset of crop damage.

Growth and Development of Populations

Knowledge of how temperatures influence the growth and development of just one insect can also be used to predict the growth and development of many insects of the same species (population). Measures used to predict the development of populations, however, necessarily differ from those that are used to predict the development of individuals. This is so because pest managers who want to predict the date on which just one larva will develop to, for example, its third instar would calculate and sum thermal units, beginning at oviposition, and declare that individual as being in the third instar on the date that summed thermal units equals the required thermal summation. For a population, however, numerous eggs will be laid over several days or weeks. Consequently, individuals that hatch from the first eggs laid will develop to the third instar sooner than will individuals that hatch from the last eggs laid. Thus, when predicting developmental events for populations, pest managers may want to determine, in the context of this example, the date on which those first larvae develop to the third instar. Other population events, such as the peak occurrence of third instar larvae, may also be predicted. This process of calculating and summing thermal units, until they reach the required thermal summation, for the purpose of predicting a population event, is called phenological modeling, and the models used for making such predictions are called phenology models. Phenology models can be constructed through the conduct of laboratory experiments or field studies.

Constructing Phenology Models Through the Conduct of Laboratory Experiments

When constructing phenology models through the conduct of laboratory experiments, several environmental chambers are used at the same time, with each being set at a different temperature. Temperatures should vary widely so as to encompass the extremes within which enzymatic activity occurs. Next, a laboratory colony of the insect is accessed, with many individuals being used in the study (experimental subjects). Then, experimental subjects are divided into as many groups as there are chambers, with each group being placed into its respective chamber. Next, all individuals are provided with sustenance (either artificial diet or a host), and monitored daily. The number of days required for each individual to grow to a given stage is then recorded. If the average or median of those days is calculated and graphed on temperatures, the resulting chart should look like that shown in the following figure (responses of experimental subjects that did not develop to the desired growth stage, at the coldest and warmest temperatures, were excluded from this graph). The upper portion of the figure (Fig. 33) shows that the number of days needed for insect growth to a given stage decreased with increasing temperatures, up to a point, after which the number of days increased; that increase was caused by temperatures being so warm that basic physiological processes were disrupted, causing retarded growth and death.

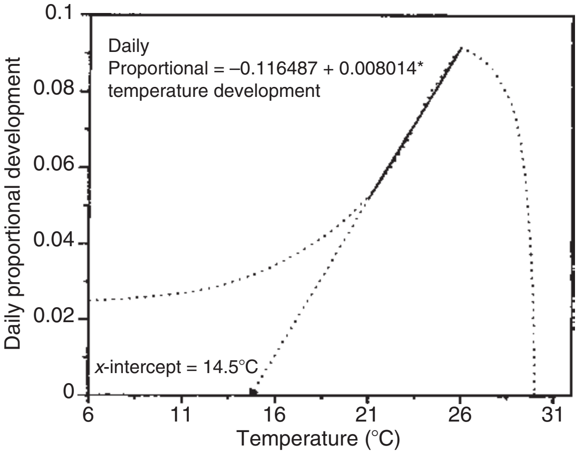


Phenology Models for Pest Management, Figure 33
Average days needed before a hypothetical insect will to develop to a certain growth stage, at various temperatures (A), and the inverse of those days (B), which expresses development on a daily basis.

Such information is not directly used to predict insect development. However, the information can be used to predict insect development if pest managers invert those values to express growth on a daily basis (the lower portion of the figure). Then, either a linear thermal unit function or a nonlinear developmental function is fitted to part or all of the data; that function is then used to predict insect phenological development.

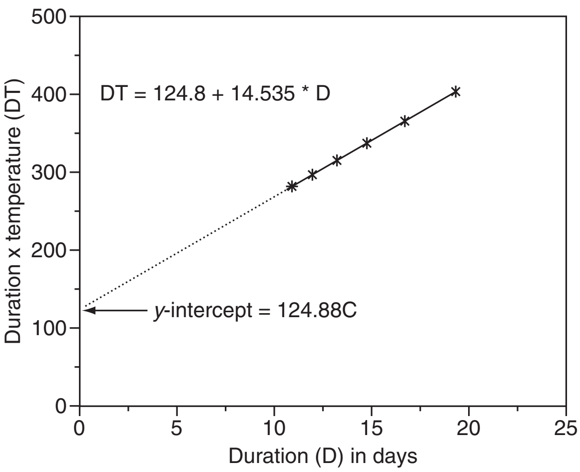
Predicting Insect Development with a Linear Thermal Unit Function

A linear thermal unit function is calculated by trimming the nonlinear portion from the relationship, and mathematically fitting a straight line to what is left. The resulting "straight line" is then extrapolated to where it crosses the x-axis (x-intercept); the temperature corresponding with that point is the developmental zero temperature or lower developmental threshold (Fig. 34). Hypothetically, that value is the lowest temperature at which insect growth will occur. Next, the required thermal summation is calculated. One way to do that is to invert the value of the slope from the straight line (i.e., 1/0.008014 = 124.8°C). Another way to do that is to multiply the effective temperature of each growth chamber (effective temperature = temperature of growth chamber–lower developmental threshold) by the average or median number of days that were required for development (Fig. 35). A third way to do that is to multiply each average or median number of days that were required for development by their respective temperature, then calculate a straight line between that product and the average or median number of days that were required for development. When that is done, the point where that line crosses the y-axis (y-intercept) (124.8°C) is the required thermal summation and the slope of that line (14.5°C) is the lower developmental threshold. Regardless of how the required thermal summation and lower developmental threshold are calculated, those values are then used to predict phenological events in the field.



Phenology Models for Pest Management, Figure 34
One way the lowest temperature at which insect development will first occur (lower developmental threshold) can be estimated is to trim the nonlinear portions from the daily developmental curve, then mathematically fit a straight line to the rest; the lower developmental threshold is the temperature where the straight line crosses the x-axis (14.5°C), and the total amount of heat needed for the insect to develop is the inverse of the slope (i.e., 1/0.008014 = 124.8°C).

That is done by first obtaining average daily temperatures from locations where the predictions are to be made. One way to do that is to add the daily maximum and minimum temperatures together, then divide that sum by two ("rectangle" method). There are other ways that can be done, one of which is to use a "sine-wave" method. Next, daily thermal units are calculated by subtracting the lower developmental threshold from the average daily temperature; if that difference is less than zero, daily thermal units are set equal to zero. Thermal units are calculated for each 24-h period and summed until they equal the required thermal summation. Theoretically, the date on which that happens is the date on which the developmental event occurs.



Phenology Models for Pest Management, Figure 35

Another way the lowest temperature at which insect development will first occur (lower developmental threshold) can be estimated is to trim the nonlinear portions from the relationship, multiply the average (or median) days to development (D) by their respective temperatures (T), and mathematically draw a straight line between that product and D; the lower developmental threshold is the slope of that straight line (14.535°C), and the total amount of heat needed for the insect to develop is the value for DT where the straight line crosses the y-axis (124.8°C).

Predicting Insect Development with a Nonlinear Developmental Function

Nonlinear developmental functions can be constructed by fitting a mathematical equation to both the linear and nonlinear portions of the relationship curve. Several such equations could be used to do this, some of which are based on theory (theoretical equations), and others are based on fitting techniques (empirical equations). In addition, some of these equations will provide estimates of the lower developmental threshold. Whichever type of equation is chosen, it is then used to calculate proportional insect development, given some measure of daily heat. Such calculations are made for each 24 h period, with those proportions being added, from 1 day to the next, until that sum equals 1.0. Theoretically, the date on which that sum equals 1.0 is the date on which the phenological event occurs.

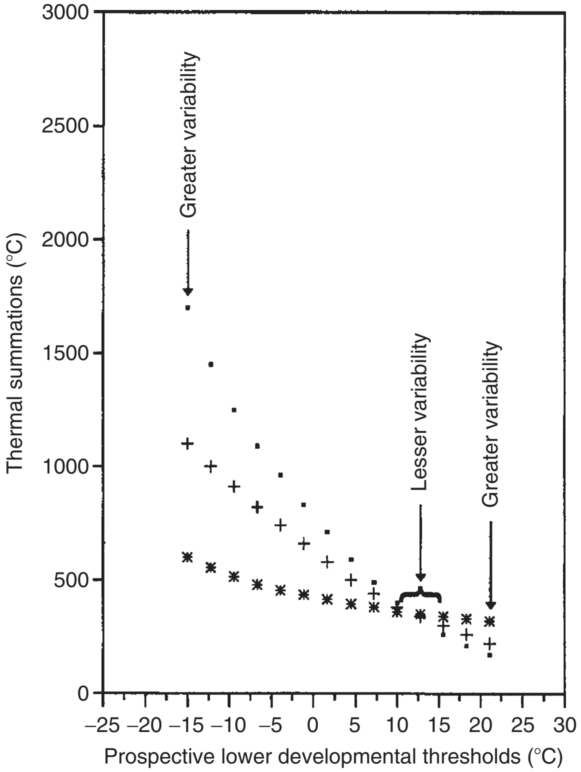
Constructing Phenology Models Through the Use of Field Studies

If the insect cannot be reared on artificial diet, or if its host cannot be grown in the greenhouse and placed in environmental chambers, then phenology models must be constructed through the use of field studies. This can be done in several ways, one of which is to find a location at which the insect is known to habit, and visit that location every day until the phenological event occurs; that date is then recorded. This process is repeated for many years. Next, daily maximum and minimum temperatures are procured from the nearest weather station, for each year the observations were made, beginning on a selected starting date and ending on the dates the phenological event occurred. These temperatures are saved in separate computer files, with each year of temperatures comprising a single file (temperature data sets).

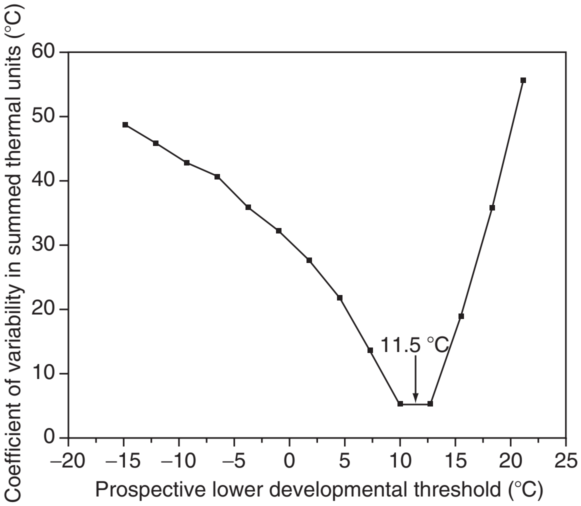
Initially, as pest managers do not know what value to use for the lower developmental threshold, several prospective values (prospective lower developmental thresholds) are chosen to calculate and sum prospective thermal units (prospective thermal summations). This is done with each temperature data set. For example, if there were just 3 years of field observations, and their corresponding temperature data sets were used to calculate prospective thermal summations with each of fourteen prospective lower developmental thresholds, a plot of prospective thermal summations on prospective lower developmental thresholds may look like that shown in Figure 36. Note that the spread between prospective thermal summations is greater at both ends of the plot.

Using this data, there are several methods by which a pest manager can actually calculate the lower developmental threshold. Two methods discussed here are the least variability and the modified regression methods. The least variability method involves calculating a simple measure of variability, or spread, in the required thermal summations, then determines the prospective lower developmental threshold(s) for which that variability is least. This approach clearly shows that prospective lower developmental thresholds which ranged from 10 to 13°C provided the least variability in the required thermal summation and, therefore, would work equally well as the lower developmental threshold. When all temperatures within a range are equally acceptable, their mid-point value is calculated (11.5°C) and used as the lower developmental threshold. Next, the chosen lower developmental threshold is used to calculate and sum thermal units, separately for each temperature data set. An average or median of those values is then calculated and used as the required thermal summation in the phenology model.

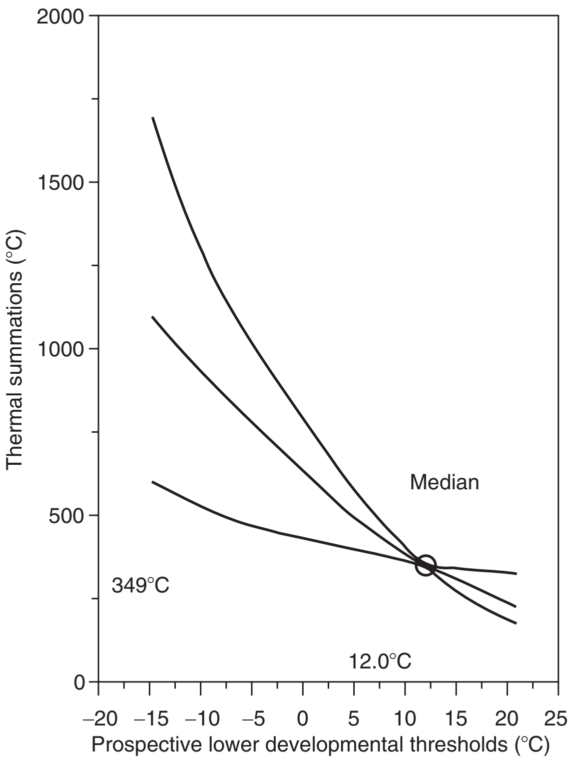
The modified regression method is used by first calculating mathematical equations that realistically express the curve-type relations; the use of such equations produces a set of curves. These equations are then used to determine mathematically where those curves cross, or have a point of closest convergence. Each such crossing point, or point of closest convergence (Fig. 38), corresponds with an individual estimate of a required thermal summation (y-axis) and lower developmental threshold (x-axis). Then, the average or median of those estimates is calculated and used in the phenology model as the required thermal summation and lower developmental threshold. The modified regression method is extremely difficult to use without the aid of a computer. Fortunately, a computer program (CALFUN) is available and can be used



Phenology Models for Pest Management, Figure 36 **Typical curve-like relations between prospective thermal summations and prospective lower developmental thresholds that are seen in the temperate climes; the area of lesser variability corresponds with estimates of values for the required thermal summation (y-axis).**



Phenology Models for Pest Management, Figure 37 **A typical plot of the variability in the data, on values for prospective lower developmental threshold (x-axis); values for prospective lower developmental threshold at which the variability was least are used as estimates of lower developmental threshold (in this case, their mid-point value, 11.5°C, was selected).**



Phenology Models for Pest Management, Figure 38 **Results from developing mathematical equations (curves) showing their generalized area of convergence (encircled area); corresponding values for prospective required thermal summation (y-axis) (349°C) and prospective lower developmental threshold (x-axis) (12.0°C) are estimates of the required thermal summation and the lower developmental threshold, respectively.**

to quickly and easily perform these calculations. CALFUN can be obtained from the World Wide Web at the following URL: http://w3.uwyo.edu/~dlegg/calfun.html.

Once values for the lower developmental threshold and required thermal summation are calculated, the value for the threshold is used to calculate daily thermal units, which are summed until the date on which that sum equals the required thermal summation. Theoretically, that is the date on which the phenological event occurs.

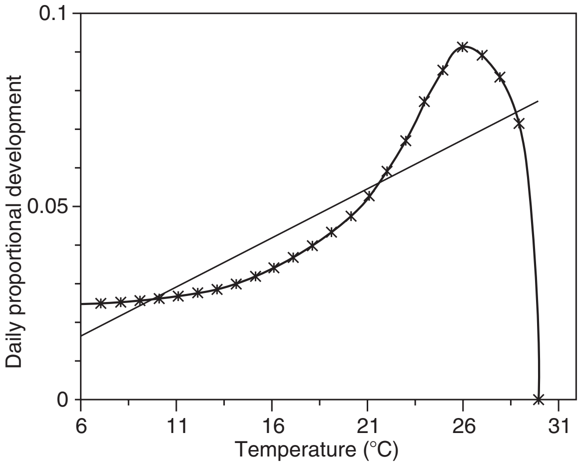
Concluding Remarks

There are advantages and disadvantages to developing phenology models in the laboratory and in the field. One advantage to developing phenology models in the laboratory is that values for the lower developmental threshold are biologically meaningful. That is, they represent temperatures at which growth and development will first occur. One potential disadvantage to developing phenology models in the laboratory, however, is that they must make use of temperatures that actually occur where the insect is found. Those places include soil, dung, fruit, and plant tissues (substrate). As phenology models often make use of air temperatures to calculate either daily thermal units or proportional daily development, it may be necessary to convert those temperatures into substrate temperatures before laboratory-based phenology models will be effective.

One advantage to developing phenology models from field studies may be that converting air temperatures into substrate temperatures will not be necessary. This is so because field-developed phenology models appear to have the air temperature-substrate temperature relationship already factored into the values that are calculated for required thermal summation and lower developmental threshold. This, however, suggests one disadvantage to calculating lower developmental thresholds and required thermal summations from field studies; their values may not be biologically meaningful.

Phenology models that are based on nonlinear thermal unit functions are sometimes thought of as being superior to those that are based on linear thermal unit functions. This is so because nonlinear thermal unit functions best describe the relation between insect growth and a wide range of temperatures. However, many insects have behaviors that, when exhibited, help regulate their body temperatures to some extent (thermal regulation). For example, many grasshoppers will climb plants to escape uncomfortably warm temperatures near the ground, or will climb plants to better impact sunshine, on cool mornings, so they will warm rapidly. Also, many grasshopper species will turn their bodies in such a way as to "bask" in sunshine, thereby keeping their cellular temperatures warmer, for longer periods of time, throughout a chilly day. Such behaviors may largely serve to keep insect growth within the linear portion of their developmental curves. If that is true, then phenology models that are based on linear thermal unit functions will be superior to those that are based on nonlinear developmental functions when predicting phenological events in the field. However, if such behaviors do not keep insect development within the linear portion of their developmental curves, then phenology models that are based on nonlinear developmental functions will be superior to those that are based on linear developmental functions when predicting phenological events in the field (Fig. 39).

Finally, the performance of many phenology models may be acceptable when they are used to predict insect phenological development in most fields, orchards, or pastures (target populations), but unacceptable in some others. Unacceptable performances may occur when the temperatures recorded at the location of a weather station do not reflect the temperatures that occur at some target populations. Such discrepancies can occur for several reasons, but most involve localized site-specific features such as soil types, plant litter, or slope of terrain relative to the angle of the sun. For some combinations of these features, the area of the target population may be warmed much more than the area of the weather station, resulting in accelerated insect development relative to the output of a phenology model that is using temperatures recorded at the weather station. For other combinations, however, the area of the target population may be much cooler than the area where the weather station is located, thus resulting in retarded insect development relative to the output of a phenology model that is using temperatures recorded at the weather station. For those target populations where such site-specific features can cause phenology models to perform poorly, it may be necessary to make use of on-site temperature recorders. The use of temperatures from these recorders should result in acceptable predictions of insect phenological events.



Phenology Models for Pest Management, Figure 39 **Results from using a linear model (straight line) and nonlinear model (curve) to describe the observed proportions of daily development (asterisks); note that the nonlinear model best describes observed daily proportional development over a wide range of temperatures.**

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Phenotype

The physical appearance of an individual that are determined by both genotype and environment (contrast with genotype).

Phenotypic Plasticity

This is the property of a genotype being able to produce different phenotypes in response to different environmental conditions. Evolution can channel organisms into a stabilized phenotype, with little plasticity, that is well developed for a certain function or environment. Alternatively, it can lead to a more flexible phenotype, producing a robust organism that varies according to environmental stimuli. This latter condition is more common than generally acknowledged. Some of these flexible or "plastic" phenotypes show gradual change in response to environmental variation, without producing discretely different subsets, and are called "reaction norms." Some phenotypes produce discretely different (lacking intermediate forms) intraspecific variation, and this is called "polyphenism." Polyphenisms (= polymorphisms) are adaptations to reliable and predictable variations in the environment.

In most cases, a genotype gives rise not to a single phenotype, but a range of phenotypes. Thus, phenotypes are a product of the genotype and the environment, and results in the expression of alternative morphology, behavior, and performance. The resulting plasticity is important in ecological and evolutionary success of the organism. Phenotypic plasticity can act as a buffering agent against environmental variation. We might expect, then, to find phenotypic plasticity most pronounced in organisms inhabiting heterogeneous environments. Phenotypic plasticity favors host race formation in insects, and sympatric speciation.

► Polyphenism
► Polymorphism in Locusts
► Polyphenism and Juvenile Hormone (JH)
► Castes

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Pheromone

Chemical substance secreted externally into the environment that affects the behavior or physiology of other members of the same species. Pheromones are a type of semiochemical.

► Chemical Ecology
► Alarm Pheromones
► Sex Pheromones

Pheromones

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When we hear the term "pheromone," our thoughts automatically turn to love! Pheromones certainly are involved in getting the sexes together (not only insects, but most animals, and possibly even humans, use sex pheromones to facilitate reproduction) but they have myriad other functions in the lives of insects as well. Males and females, sometimes both sexes, within a species may produce pheromones to coordinate their life histories. Simply defined, pheromones are one type of semiochemical (chemical compound that mediates interactions between organisms) that carry information between organisms of the same species. The term is derived from the Greek verbs "pherein" (to carry) and "horman" (to excite or to stimulate). Thus, pheromones are chemical substances that, when secreted to the outside of an organism, cause a specific reaction in a receiving organism of the same species.

Types of Pheromones

Pheromones can be classified by the effect that they have on the receiving organism. They may be "releaser" pheromones, where the receiving organism immediately performs a stereotypical behavior or sequence of behaviors upon perceiving the pheromone. For example, when flying male moths perceive the volatile, sex attractant pheromone of a female moth, they immediately turn upwind, and begin casting, a flight behavior characterized by large-amplitude horizontal excursions with no forward movement. This behavior, and the subsequent upwind flight, help them locate the source of the odor, which is the virgin female. The second type of pheromone is a "primer" pheromone. These pheromones set in motion complex physiological changes, such as development or sexual maturation, in the receiving organism. For example, mandibular gland pheromone produced by queen honeybees inhibits initiation of queen rearing and regulates division of labor in the worker caste through effects on the worker bees' juvenile hormone levels.

Pheromones may be categorized based on the function they appear to have in the insect. For example, chemicals released by an insect under attack by a predator may be termed an alarm pheromone if other individuals of the same species react to it by dispersing, running around frantically, jumping off the plant, or displaying some other type of alarmed behavior. Many types of pheromones have been described based on their supposed function in a species: sex attractant pheromone, courtship pheromone, marking pheromone, oviposition deterrent pheromone, aggregation pheromone, and the many pheromones used in the lives of social insects for the purposes of recruitment, nest-mate recognition, and trail laying.

The Early Days of Pheromone Research

The history of pheromone research is relatively recent. It has been observed since the 1700s that male moths are attracted to female moths of the same species. Jean-Henri Fabre, a French naturalist active in the late 1800s, was the first to perform experiments to test the attraction of male moths to females and to suggest a mechanism to explain his observations. His experiments began after a chance observation, as great scientific discoveries often do. He was keeping a pupa of the Great Peacock moth, *Saturnia pyri*, in his office. One day the moth enclosed and it happened to be female. That night he and his young son went into his office and, because the window had been left open, found twenty male *S. pyri* moths fluttering about the room. He originally thought that the virgin female moth was producing some sort of X-rays or some form of "etheric" waves to signal males. However, after several years of experiments with this species, and several others, he concluded, as astounding as it seemed to him, that female moths were producing an odor that was attractive to males from a great distance.

It was not until the epic research of German chemists, Adolf Butenandt and his colleagues, that the first pheromone was identified. This group was interested in the potential use of insect sex pheromones in management of agricultural pests. They began isolating the sex attractant pheromone of the silkworm moth, *Bombyx mori*, in 1939, choosing this beneficial lepidopteran as a model because of the ease of obtaining large numbers of insects for chemical isolation. Twenty years, and 500,000 female moths later, they had succeeded in isolating and identifying one component of the silkworm's female-produced sex attractant pheromone, which they termed "bombykol." Their success was remarkable because of the meager tools that these analytical chemists had at their disposal. They were dealing with much smaller amounts of chemicals than were analyzed routinely at the time. Today, insect pheromones often can be isolated, identified and synthesized within 6 months, depending on their complexity. Amazingly, with today's analytical instrumentation (gas chromatographs and mass spectrometers), we can measure easily the amount of pheromone a single female insect releases over only an hour's period of time.

Pheromone Biosynthesis

Many insects biosynthesize their pheromones de novo, meaning that they break down their food into small molecules which they then use as the building blocks for their pheromones. For example, the female-produced sex attractant pheromones of most moth species analyzed so far are straight-chain hydrocarbon molecules with oxygen-containing functional groups (alcohols, aldehydes and acetates), varying in length from 8 to 18 carbon atoms. The molecules usually are made by the end-to-end addition of acetate molecules, two-carbon-atom building blocks which are end-products of fatty acid metabolism.

Other insects however, biosynthesize their pheromones from specific plant-derived molecules, processing them only minimally before use as a pheromone. This occurs commonly in several species of ithomiine and danaiid butterflies (like the monarch butterfly) and tiger moths (family Arctiidae). In these species, the male butterfly sequesters plant compounds, either from its larval food or, as an adult, from plant species that are visited solely for the purpose of collecting these molecules, and modifies them slightly for use as an aphrodisiac or courtship pheromone. These pheromones are produced in specialized glands at the tip of the male's abdomen and are either sprinkled on the female or wafted in front of her from modified scales called hair pencils or inflatable, eversible sacs called coremata. Perception of the courtship pheromone may allow the female to judge the fitness of the courting male and will result in mating if she deems him "fit."

Pheromone components may be made, not by the insect itself, but by symbiotic microorganisms that live within the insect's body. For example, the spruce bark beetle, *Ips typographus* (family Scolytidae), a devastating pest of forest trees in Europe, has a symbiotic relationship with yeast fungi. When pioneer beetles first attack healthy trees, they release a multi-component aggregation pheromone that attracts more beetles to help overwhelm the tree's sticky and toxic resin defense. One of the components of this aggregation pheromone (cis-verbenol) is produced as a detoxification product of a terpene defensive compound in the tree (α-pinene) by yeast found in the hindgut of the colonizing beetles. After there is adequate colonization of the tree and its defense has been breached, the yeast transforms cis-verbenol to verbenone, which acts as an anti-aggregation pheromone stopping further colonization and reducing the negative effects of beetle overcrowding and competition.

Finally, some insects may use plant compounds directly as pheromones without further modification. The euglossine orchid bees (family Apidae) are pollinators of orchids in the New World tropics, with each species of bee usually visiting and pollinating only one species of orchid. In this group of bees, the males, never the females, pollinate the orchids. The bees gain no nectar or pollen reward but instead collect large quantities of fragrances that the orchids produce. These fragrances are stored in specialized organs in the hind femora of the bees and are hypothesized to be used to facilitate mating. The stored orchid volatiles attract other male bees to a mating display, or a lek, to which female bees are subsequently attracted. Females at these leks can possibly choose specific males to mate with based on the quality or quantity of the orchid fragrance they have collected.

Pheromones are made in exocrine glands, specialized glands that are found on various portions of the body, usually in the epidermis. The glandular secretions are released to the outside of the body. Pheromones usually are released only at certain times of the day or night based on an internal biological rhythm. Most pheromones are volatile, small molecules borne in the air and are perceived by olfactory chemoreceptors on the antennae. Some pheromones are larger, less volatile, or even nonvolatile, molecules that are perceived by contact chemoreceptors found on the ovipositor, antennae, and elsewhere.

Use of Pheromones by Insects and Humans

Chemical communication via pheromones has tremendous benefit to insect species that may not have extensive adaptations for visual or acoustic communication. Thus, pheromone production is extremely common and widespread among the class Insecta. However, there are costs associated with the production of pheromones. One of the major costs is the fact that many predatory and parasitic insects have evolved the ability to perceive these pheromones and can eavesdrop on the communication going on between members of their prey species. For example, several species of predaceous clerid beetles are attracted to the aggregation pheromone of bark beetles. Species of *Trichogramma*, minute hymenopterans that often parasitize the eggs of Lepidoptera, are attracted to the sex attractant pheromone of female moths. Female parasitoids of several species of tephritid fruit flies are stimulated to search a fruit for hidden host larvae when they perceive the nonvolatile host-marking pheromone laid down on the fruit by the ovipositing female fruit fly. Some species of predator have even evolved the ability to produce the pheromone of their prey and thus lure their prey to them. For example, the females of several species of bolas spiders, *Mastophora* spp., produce the sex attractant pheromone of the females of the moth species on which they prey. When the male moth approaches the bolas spider, expecting to find a virgin female moth, he is captured by a sticky bolas that the spider launches at him.

The list of such examples of illicit communication is endless and illustrates the fascinating odorous world in which insects live, and of which we humans largely are unaware due to our poor sense of smell. Despite being unable to directly experience this hubbub of chemical communication, we have taken advantage of it to help control pestiferous insects that harm our food supply. We have used insect pheromones to detect the presence of pest insects as an early warning of their immigration into an area, to time insecticide applications or other control measures, and to document arrival of quarantine pests in pest-free areas. Pheromone monitoring also can be used to quantify insect populations or, at least, to indicate whether populations are declining or increasing. We have used pheromones to disrupt insect's mating behavior. For example, the pink bollworm, *Pectinophora gossypiella*, an economically important pyralid moth pest of cotton in both the Old and New World, is managed almost exclusively now by the area-wide application of Gossyplure, a synthetic version of the female's sex attractant pheromone. The pheromone is formulated for slow release and is dispersed over large acreages of cotton. The multiple point sources of pheromone in the field make it very difficult for the male bollworm moth to find virgin females and mate with them, thus slowing population increase and the associated yield loss.

Pheromones also are used in mass trapping and attract and kill strategies. In mass trapping of bark beetles for example, large vertical funnel traps are baited with aggregation pheromones. Bark beetles are attracted to the tall, cylindrical funnel traps (which visually mimic trees) and are trapped in the funnels, thus taking them out of the population. In the attract and kill strategy, insects are attracted to a pheromone-impregnated substrate that also has been treated with an insecticide or sterilant so that the insects are excluded from the breeding population. The addition of the house fly sex pheromone, (Z)-9-tricosene, to granular food baits impregnated with an insecticide greatly improved control of house flies in commercial animal production facilities over use of an insecticide-treated food bait alone.

To date, the majority of pheromones that have been used in pest management are female-produced sex attractant pheromones and bark beetle aggregation pheromones. Other pheromones that have potential are the anti-aggregation pheromones of bark beetles that may have potential to prevent infestation of trees, oviposition-deterring pheromones of fruit flies and other insects to prevent oviposition in crops, and alarm pheromones of aphids that increase aphid movement in the area of the alarm pheromone, thus making the aphids more likely to contact a lethal dose of insecticide or to be noticed by visually orienting predators or parasitoids.

- ► Social Insect Pheromones
- ► Alarm Pheromones
- ► Sex Attractant Pheromones
- ► Marking Pheromones

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Pheromone Parsimony

A phenomenon wherein the same pheromone can serve multiple functions. For example, a marking pheromone may also function as an aggregation pheromone, an antimicrobial agent, and a kairomone.

Phialides

Specialized cells with one or more open ends from which conidia are produced in basipetal succession. Thus, the apical conidia are the oldest.

Philanthidae

A family of wasps (order Hymenoptera).

- ► Wasps, Ants, Bees and Sawflies

Philopotamidae

A family of caddisflies (order Trichoptera). They commonly are known as finger-net caddisflies or silken-tube spinners.

- ► Caddisflies

Philopteridae

A family of chewing lice (order Phthiraptera). They sometimes are called bird lice.

- ► Chewing and Sucking Lice

Philotarsidae

A family of psocids (order Psocoptera).

- ► Bark-Lice, Book-Lice and Psocids

Phlaeothripidae

A family of thrips (order Thysanoptera).

- ► Thrips

Phloeidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

- ► Bugs

Phoenician Billbug, *Sphenophorus phoeniciensis* Chittenden (Coleoptera: Curculionidae)

This turfgrass pest affects grass in the southwestern USA.

- ► Turfgrass Insects and Their Management

Phoenicococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called palm scales.

- ► Scale Insects, Mealybugs
- ► Bugs

Phonotaxis

Taxis response with respect to sound.

Phoracantha longicorn Beetles (Coleoptera: Cerambycidae)

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New Zealand

The genus *Phoracantha* Newman belongs to the family Cerambycidae of the order Coleoptera.

Order: Coleoptera
  Family: Cerambycidae
    Subfamily: Cerambycinae
      Tribe: Phoracanthini
        Genus: *Phoracantha*

External Morphology

Phoracantha adults range from 14 to 48 mm in length. Body is pale, yellowish, reddish to blackish brown with elytra having colored fasciae in most species, usually zigzag, arranged transversely. At least antennal segments 3–6 are unispined or bispined at apex. The prothorax is wider than long, with depressed hairs, and the pronotum has a spine or strong prominent conical process at each side. The elytral apex is usually bispined, at least spined at marginal angle. The femora are lineate or gradually thickened. Larvae have an elongate, cylindrical body shape.

Biodiversity and Distribution

Phoracantha has 40 known species and is the most speciose genus of the tribe Phoracanthini. This genus is mainly distributed in southern Australia, and some species occur in northern Australia and New Guinea. Only two species are endemic to Papua New Guinea. In Australia, these beetles are predominantly along the coast, with only one species, *P. tuberalis*, restricted to the center of the Australian continent. About eight widely distributed species occur in both coastal and central areas. Several species are known to be introduced to other parts of the world, for example, *P. semipunctata* and *P. recurva* now occur in all zoogeographic regions except the Oriental Region.

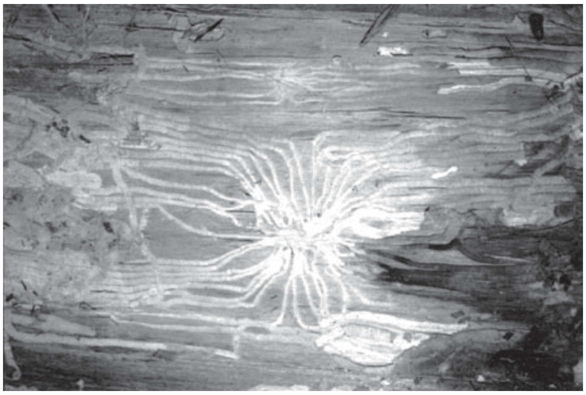
Habitat, Host and Life Cycle

Many *Phoracantha* species are associated with the tree genus *Eucalyptus* and a few with *Acacia*. Adults are active during the night, hiding in daytime under loose bark or in crevices, and can be attracted by light. Larvae bore into trunks or branches of trees. Biologically, the borers can be divided into two groups: (i) dead/dying tree consumers, including *P. semipunctata*, *P. recurva*, *P. tricuspis* and *P. punctata*, and (ii) living tree consumers, including *P. mastersi*, *P. acanthocera*, *P. frenchi*, *P. impavida*, *P. synonyma*, *P. solida* and *P. odewahni*. These are clearly defined functional groups, and the species can be allocated clearly to one or other of these (Figs. 40–42).

The members of the dead/dying tree consumers have 1–2 generations a year, attacking newly felled and dying trees, of all ages, of *Eucalyptus* species. More than 50 eucalypt species are host plants of this group. The group is distributed in both northern and southern parts of Australia. Adults lay eggs in large batches under loose bark, or in crevices, with each egg mass consisting of 23–340 eggs. The larvae feed in and under the bark for 2–6 months, making regular tunnels up to 1.5 m long, either in a straight line or twisted, radiating from the egg mass in all directions. When mature, the larvae bore into hardwood to pupate at a depth of up to 20 cm from surface. In general, this group of consumers damages trees because of the large number of larvae produced.

The living tree consumers need from 2 to 3 years to complete their life cycle. They attack living trees of all ages, but particularly young trees aged from 6 to 20 years. They have a much narrower

Phoracantha longicorn Beetles (Coleoptera: Cerambycidae), Figure 40 ***P. recurva*** **adult.**



Phoracantha longicorn Beetles (Coleoptera: Cerambycidae), Figure 41 **Tunnels in a eucalyptus tree made by** ***P. semipunctata*****.**

range of host plants than the dead/dying tree consumers, only about 20 eucalypt species have been recorded as their hosts, with each longicorn species having its own eucalypt hosts. In addition, they are distributed in either southern or northern parts of Australia. Eggs are laid singly or in only

Phoracantha longicorn Beetles (Coleoptera: Cerambycidae), Figure 42 **Tunnel in a eucalyptus tree made by** ***P. acanthocera*****.**

small batches, in bark cracks or the sites of injuries, with each egg mass consisting of 1–18 eggs. The larvae do not make the radial or parallel tunnels as dead/dying consumers do, but their activities make 1–6 large damaged areas under the bark and they may bore into the hardwood several times before pupating there. In general, one tree supports only one species of living tree consumers, and one or a few larvae. In many cases, even a couple of larvae can kill a tree.

Insect Natural Enemies

Insect natural enemies cause substantial mortality of *Phoracantha*. Parasitoids are mainly recorded from Hymenoptera, including three families and

13 species. The genera *Callibracon*, *Syngaster* and *Jarra* of Braconidae are major larval parasitoids and *Avetianella* from Encyrtidae is the only known egg parasitoid of *Phoracantha*. Some of these parasites have been introduced to North America and South Africa for biological control of *P. semipunctata* and *P. recurva*. Known predators are mainly from coleopteran families Cleridae and Colydiidae. The clerid genera *Stigmatium*, *Trogodendron* and *Tenerus* attack *Phoracantha* larvae, and the colydiid genera *Bothrideres*, *Deretaphrus*, *Phormesa* and *Teredalaemus* prey on either adults or larvae. *Stigmatium gilberti* was observed to feed on *Phoracantha* eggs as well.

Economic and Ecological Importance

Most phoracanthine species of economic importance are placed in this genus and some species are serious pests of eucalypt forests in various states of Australia and many countries around the world. The widely distributed species are more likely to become pests in Australia and elsewhere. For example, *P. semipunctata* and *P. recurva* have now been established in many countries in Africa, South and North America, and the Mediterranean region, and have become serious pests of *Eucalyptus* plantations in these regions. They feed mainly on dead or stressed trees, and can survive lengthy shipment in logs between continents. Other species such as *P. obscura*, *P. punctata* and *P. tricupis*, have similar necessities and life cycles and can cause serious damage to *Eucalyptus* outside Australia if introduced. The dead/dying tree consumers are important in recycling dead and sickly trees in nature and promoting re-growth of forest.

The species *P. solida*, *P. synonyma*, and *P. acanthocera* have wider geographic adaptation than most other *Phoracantha* species, and have become pests of Australian *Eucalyptus* forests. Of these species, *P. acanthocera* has become a serious pest in all southern states of Australia. Because these species mainly live on healthy trees, they may not be able to survive lengthy shipment in logs. So far, none of them has been reported to have established outside Australia. However, if these species are accidentally introduced into other regions, they may be more harmful than dead/dying tree consumers to *Eucalyptus* plantations. Species other than those mentioned above appear not to be able to adapt to a wide range of environments and are less likely to become important pests in Australia or other countries, except one species, *P. mastersi*, which is a fairly serious pest in southeastern Australia, particularly in Tasmania.

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Phoresy

A symbiotic relationship with transport of one organism by another. Phoretic relationships display little or no pathology to the host. Many insects, nematodes, and microbial organisms have phoretic associations with insects.

Phoridae

A family of flies (order Diptera). They commonly are known humpbacked flies.

► Flies (Diptera)
► Myiasis

Phryganeidae

A family of caddisflies (order Trichoptera). They commonly are known as large caddisflies.

► Caddisflies

Phosphorylation

The combination of phosphoric acid with a compound. Many proteins in eukaryotes are phosphorylated.

Photodynamic Action in Pest Control and Medicine

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In most cases, life depends on light. For instance, photosynthesis (the process by which plants derive the energy needed for growth) provides almost all food for both humans and animals. Light has profound implications for the field of medicine. While it works as a cause of disease (e.g., UV damage of DNA) it also may be applied as a therapeutic agent (cf. photodynamic therapy). Additionally, light also acts as a means for plant defense against herbivorous animals including insects.

In contrast to the normal photobiological processes that are essential to the physiology of living organisms such as photosynthesis in green plants, biological systems also can be damaged and destroyed by non-physiological photochemical reactions after light absorption. These reactions are the result of the interference of certain dyes and many secondary plant products known as photosensitizers that are carried out either in the presence or the absence of oxygen. The latter category, which is realized under anaerobic conditions, is much less common.

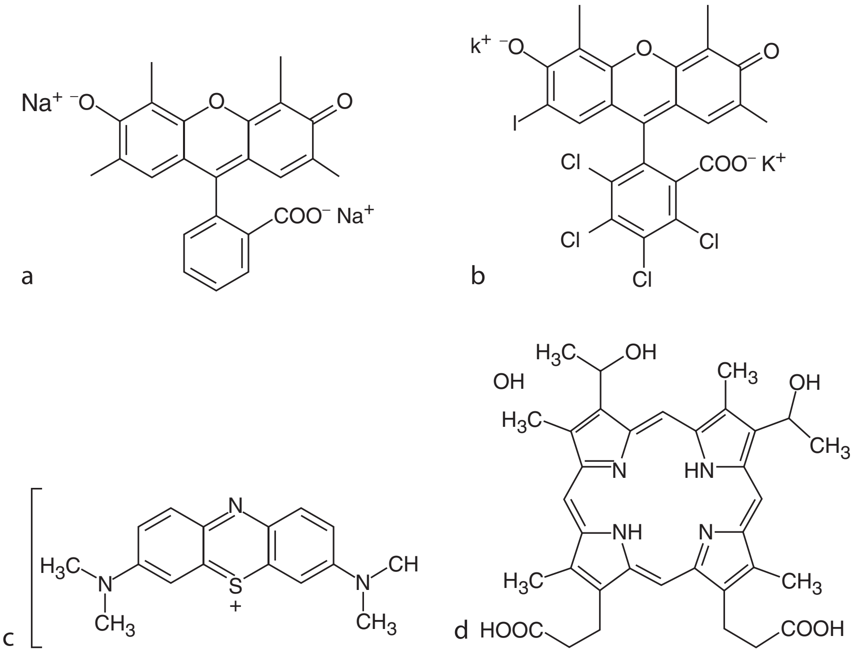
The question of potential hazards to humans arises with the wide use of photodynamic sensitizers in foods, drugs and cosmetics. In addition, there is considerable experimental evidence on the photodynamic effects of several popular dyes as highly active insecticides, and some clear evidence for photocarcinogenicity of certain phototoxic agents (Fig. 43).

The term photodynamic action or "photodynamische Erscheinung" was suggested in 1904 by Tappeiner and Jodlbauer to differentiate this activity from the photosensitization of photographic plates by dyes. Much later, Spikes and Glad defined photodynamic action as the killing or damaging of an organism, cell, or virus, or the chemical modification of a (bio-) molecule in the presence of a sensitizing dye and molecular oxygen. However, considering recent discovery of the photodynamic action in some important groups of phytochemicals, such as furanocoumarins, polyacetylenes and their thiophene derivatives, cercosporin, hypericin, and numerous photosensitizing drugs, which exclusively work at the near UV range (300–400 nm), it is apparent that photodynamic action is not limited to dyes, but includes many biomolecules (Fig. 44).

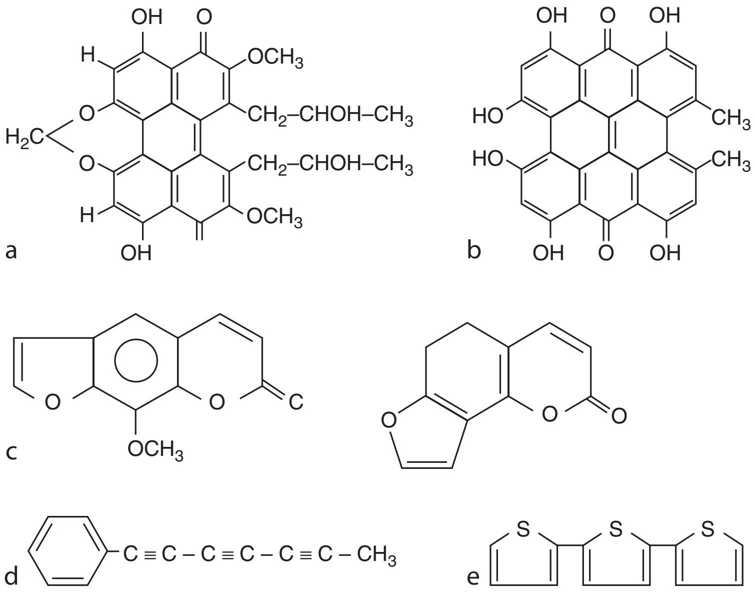
O_2 Metabolism

The oxidative processes that are fundamental to photodynamic action differ greatly from normal cellular metabolism. Differences include:

1. While the respiratory quotient, i.e., the ratio between CO_2 production and O_2, is near unity for normal aerobic metabolism, the ratio during photodynamic action is up to 20-fold lower than the former (e.g., 0.048 vs 1.00).
2. Normal O_2 metabolism is virtually abolished if the structure of the cell is destroyed. Whereas, the O_2 uptake during photodynamic action has been found to remain the same for both intact or hemolyzed red blood cells.
3. While cyanide inhibits normal O_2 metabolism, it increases the uptake of O_2 in photodynamic action.
4. Normal O_2 metabolism is destroyed by heat, whereas boiling does not abolish the photosensitized uptake of O_2.



Photodynamic Action in Pest Control and Medicine, Figure 43 Some examples of several dyes with photodynamic action: i.e., halogenated dyes – e.g., (a) Erythrosin ($C_{20}H_6I_4Na_2O_5$), (b) Rose Bengal ($C_{20}H_2Cl_4I_4K_2O_5$) and (c) Methylene Blue ($C_{16}H_{18}Cl$-N_3S); and non-halogenated dyes – e.g., (d) Hematoporphyrin ($C_{34}H_{38}N_4O_6$).



Photodynamic Action in Pest Control and Medicine, Figure 44 Chemical structures of several secondary plant products with photodynamic action: (a) cercosporin; (b) hypericin; (c) furanocoumarins (left, linear: e.g., 8-methoxypsoralen, i.e., 8-MOP or xanthotoxin; and right, angular: e.g., angelicin); and finally polyacetylenes (e.g., phyenylheptatriyne) and their thiophenes – e.g., α-terthienyl (d and e, respectively).

Light Absorption

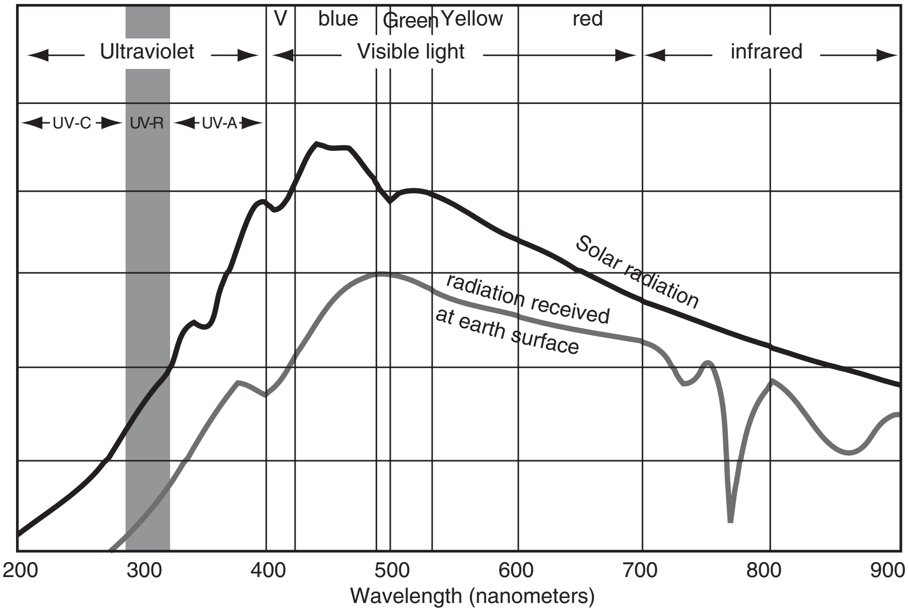
The first step of photodynamic action is absorption of light by a sensitizer (Fig. 45).

An important aspect of the photodynamic effect is that the active wavelengths are longer than 300 nm. Therefore, it is restricted to the regions of the electromagnetic spectrum that penetrates the Earth's atmosphere: i.e., some parts of the UV (300–400 nm), and entire spectrum of the visible light (400–700 nm). The destructive effect of the short-wave lengths (less than 300 or 330 nm) are well documented. However because the ozone layer absorbs almost all energy below 280–290 nm, the destructive region of solar light is confined to a narrow range (i.e., 280–330 nm).

The extent of penetration of ultraviolet (UV) and visible radiation into skin varies considerably. While UV-C (200–280 nm) does not penetrate beyond the epidermis, UV-B (280–320 nm) and UV-A (320–400 nm) enter the dermis; and visible light penetrates further into the subcutaneous tissue. UV penetration into tissue is estimated at less than 0.1 mm, whereas the typical penetration depth in living tissue of the red light used for photodynamic therapy ranges between 1 and 3 mm.

Mechanisms

When the absorption of a quantum of radiation excites a sensitizer, the energy imparted by this excitation is related to wavelength by the following equation: E = hv, where E is the energy of radiation, h is Planck's constant (i.e., 2.8591), and v is the frequency of the radiation. On the other hand, as v = c/Λ, where c is the velocity of light and Λ the wavelength, one can substitute to obtain E = hc/Λ (i.e., 2.8591 × 10^5/Λ). From this relationship, the energy imparted at a given wavelength can be determined. Basically, the shorter the wavelength, the higher the energy. At 300 nm, for example, 95.3 kcal/mole would be imparted to the molecule, which is sufficient to disrupt most covalent



Photodynamic Action in Pest Control and Medicine, Figure 45 Solar radiation and its participating spectra received at the Earth's surface: i.e., (1) ultraviolet (≤400 nm), (2) visible light including violet (abbreviated by V; ca. 400–420 nm), green (420–490 nm), yellow (490-ca 600 nm) and red (600–700 nm), and finally (3) infrared (700–900 nm). Adapted from The Ozone Layer (UNEP, Nairobi, 1987).

bonds. Basic to any energy transfer is that the molecule in question must exhibit an absorption spectrum at the wavelengths of excitation, and this absorption generally follows Beers law ($I = I_0 10^{-Ebc}$).

Phytodynamic action begins when a sensitizer (Sens) absorbs light, giving an excited state (Sens*), often (but not always), the triplet. Sens* can either react directly with the substrate (Type I reaction; less common) or with oxygen (Type II reaction). Therefore, high substrate concentrations (as well as electron-rich or hydrogen-atom-donating substrates) promote Type I reactions and high oxygen concentrations favor Type II reactions. Furthermore, in biological systems, where binding of sensitizer to substrate is common, Type I reactions are particularly favorable. While a type I reaction results in hydrogen atom or electron transfer, yielding radicals or radical ions, a type II reaction leads mainly to singlet molecular oxygen by energy transfer.

Singlet oxygen can be produced in high yield in the Type II reaction by energy transfer from Sens*. It is an electronically excited state of oxygen, with a lifetime that varies about 3–4 μs in water and as long as 0.1 s in solvents with no hydrogen atoms. In biological lipids and membranes, it probably has a lifetime considerably shorter than that in most organic solvents because of quenching by proteins and escape from the membrane into cytosol. The mechanism of action of the halogenated xanthene dyes such as rose bengal and erythrosin is considered to occur by a Type II mechanism.

The dye photosensitizer does not enter into the toxic reaction. The photosensitizer is a catalyst, not a participant. A single dye molecule is able to cycle through light absorbance, movement to the excited singlet state, transfer to the excited triplet state, sensitization of the ground state oxygen to the excited singlet state, and eventual return to the ground singlet state of the dye in approximately 10 ms, or less. It is then possible that a single dye molecule could be responsible for the generation of thousands of molecules of singlet oxygen per minute. A single dye molecule is then capable of initiating oxidation reactions which can destroy thousands of different target molecules rather than the single target molecule destroyed by a single organophosphate molecule, for instance.

Photodynamic action (photochemical damage by oxygen) is caused by oxidation of biological target molecules, and can lead to (i) membrane lysis by oxidation of unsaturated fatty acids and cholesterol, (ii) enzyme deactivation by oxidation of amino acids (methionine, histidine, tryptophan, tyrosine and cysteine), and (iii) oxidative destruction of nucleic acid bases (primarily guanine).

The responses of living organisms to photosensitized modification are varied, ranging from mild irritation to death. The precise nature of the response depends on many factors, but the majority of cases can be explained based on the changes produced in individual cells. Cellular photomodification is in fact a multi-step process which is carried out in six steps.

Step 1: The photosensitizer must get to the target cell. This involves introduction into the organism during feeding, via injection or diffusion. Once in the organism, the photosensitizer may be carried in combination with proteins, lipoproteins, or other molecules. At the target cell, the photosensitizer may need to diffuse through a vascular wall, a cell wall and/or a cell membrane. Ultimately, it must localize at or near the site of photomodification. Variations in any of these processes can significantly alter the final effect.

Step 2: Once the sensitizer has reached its site of action, it may remain free or may be bound to various biomolecules. It can also be metabolized to a form that may be more effective or less effective as a photosensitizer. The use of precursors, such as δ-aminolevulinic acid which is metabolized by the organism to a photosensitizing porphyrin, is an example of this possibility.

Step 3: At the site of action the sensitizer must be able to absorb light. This ability can be altered by the environment and physical state of the sensitizer in the organism. Binding, aggregation, metabolism and altered dielectric constant (as in a lipid membrane) are all variables that may significantly alter the absorption spectrum of the sensitizer.

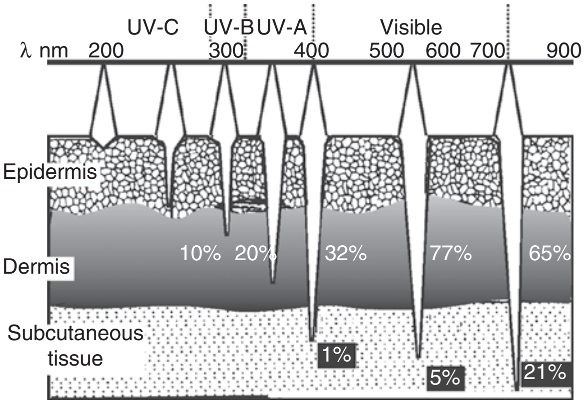
Step 4: After absorbing light, the sensitizer must make use of the energy in a way that effects a change in the cell. It may transfer energy to oxygen creating an electronically excited state such as singlet oxygen, which can then react with a cellular structure nearby. Alternatively, it can react directly with cellular biomolecules. But, in the cellular environment, it may also be quenched by the impressive array of antioxidants available in cells. Therefore, the excited state properties and reactivities of photosensitizers in vivo will not always be the same as they are in simple solution.

Step 5: The next step is the reaction of either the excited state sensitizer or a reactive intermediate, such as singlet oxygen, with cellular biomolecules which critically impair cell function and/or survival. Many biomolecules and cellular structures are photomodifiable, but not all of these affect cells in ways that result in cell death or irreparable damage. For example, it has been known for many years that cell lipids are peroxidized by photosensitized modification, but a definitive link between that peroxidation and cell killing has remained elusive.

Step 6: Finally, if enough critical cells in an organism are affected, then the foregoing steps will result in death or impairment of function. While each of these steps is critical and can significantly affect the degree of cellular modification, an in-depth analysis of Step 5 follows, namely the reactions of photosensitizer and light which lead to the critical impairment of cell function.

Effects of Photosensitizers and Light on Cells

Photosensitizers and light can affect a variety of biomolecules and cellular structures. Proteins, lipids and nucleic acids are all susceptible to photomodification. Carbohydrates are much less sensitive. This means that direct effects on cellular energy stores in the form of glucose or glycogen are unlikely to be significant. Conversely, effects on enzymes, nuclear DNA and lipid membranes may be important. Several sensitizers are accumulated in lysosomes where they may sensitize swelling and increase permeability of the lysosomal membrane allowing enzymes to be released from the lysosome. Other sensitizers seem to localize in mitochondria where they cause swelling and can affect the function of membrane-bound enzymes involved in energy production for the cell. Finally, a large variety of sensitizers, including many of the porphyrins and xanthene dyes, localize in the plasma membrane (and perhaps other membranes) altering the permeability properties of the surface membrane of the cell when illuminated, either by affecting membrane proteins or lipids. To summarize, photodynamic action involves photooxidation of various substrates which results in inactivation of biological systems, distortion of membranes, inactivation of enzymes, photocarcinogenesis, cell death and losses in other functions (Fig. 46).



Photodynamic Action in Pest Control and Medicine, Figure 46 **Extent of penetration of ultraviolet (UV) and visible light into human skin. The drawing is from the late BE Johnson, Department of Dermatology, University of Dundee (Scotland, UK). Courtesy of Springer Verlag and the editors of Photosensitization: Molecular, Cellular and Medical Aspects (G Moreno, RH Pottier, TG Truscott: 1988).**

How Do Photosensitizers and Light Kill Cells?

The above-mentioned effects of photosensitizers and light on cells offer many possible means by which a cell may be killed. Lysosomes may release degradative enzymes into the cytoplasm, mitochondrial production of ATP may be inhibited, plasma membrane barrier function may be compromised, and DNA damage may prevent cell replication and/or impair transcription required for protein synthesis and normal cell function. But some of these effects are critically related to cell death and others are merely consequences of the process of cell death.

Presently two major forms of cell death are recognized. One form, known as necrotic death or necrosis, is a degenerative cell death resulting from severe cell injury. The second form, known as apoptotic death or apoptosis, is a programmed cell death which is a cellularly controlled process. The death can occur under pathological conditions, such as cell injury, but also appears to be the mechanism by which organisms delete certain cell populations when they are no longer needed in the developmental process. While a hallmark of apoptosis is a selective cleavage of DNA, necrosis produces a random degradation of DNA.

An increase in intracellular calcium concentration has been suggested as the trigger of both forms of cell death (i.e., apoptotic and necrotic). Even cells which tolerate transient elevation of intracellular calcium concentration as part of their normal function, e.g., contracting cardiac cells where such elevation of calcium serves as the trigger for contraction, cannot tolerate this increased concentration continuously. It is well known that cardiac cells are susceptible to destruction by calcium overload. It has been documented that cellular photosensitization produces cell death by an apoptotic mechanism. Although apoptosis is a carefully orchestrated series of reactions within the cell leading ultimately to death, calcium is the trigger for this process. Thus, one should look for the mechanism that can increase intracellular calcium concentration as the seminal effect of photosensitization. As it is known that cell membranes are responsible for maintaining the very low calcium concentrations inside normal cells, i.e., 10^{-7} M, an obvious way for such increase is by a change in membrane permeability to calcium.

Multiple Mechanisms of Xanthene Dyes in Insects

Based on the foregoing studies on the toxicity of several xanthene dyes on insects, multiple mechanisms should be considered: e.g., light dependent mechanism, light independent mechanism and developmental toxicity mechanism.

Light dependent mechanism (or photodynamic action) in insects involves the ingestion of the dye by the insect, followed by exposure to a visible light source which results in the death of an insect. It is quite fast and needs comparatively lower concentrations of the photosensitizer and a source of light. In contrast, the light independent mechanism is slow, needs a higher concentration of sensitizer and operates in the absence of light.

In the developmental toxicity mechanism, the insect is exposed to a sublethal dose of the compound in the earlier stages of development. This results in mortality or some adverse morphological abnormalities during development, such as delayed development, growth retardation, and changes in fecunditiy and fertility.

Photodynamic Dyes

With the exception of hematoporphyrin, a substance known to be derivable from hemoglobin or hemin, other dyes studied for their photodynamic action are mainly confined to the synthetic dye molecules with halogenated structures.

The first documented (although qualitative) study in which light was understood to cause an enhancement of a chemically induced toxic effect was that of A. Marcacci in 1888. He reported that alkaloids were more effective against seeds, plants, fermentations, and amphibian eggs in sunlight than in the dark. This appears to be the first formal report that some materials have a light-enhanced toxic effect, even though a few dyes were already used for their anti-bacterial properties without recognition of the involvement of light action.

In 1900, a study on the toxicity of a dye (acridine) toward paramecia reported the results of the first quantitative studies on photodynamic action. Low concentrations of acridine and other dyes (at 50 ppm), which had no effect on microorganisms such as paramecium in the dark, were found to lead to a rapid death on illumination in the presence of oxygen. An increase of 2–3 orders of magnitude in the acridine sensitized mortality of paramecia was recorded. Also, those light rays which generated the greatest fluorescence in the dyes induced the largest biological reaction.

Following this discovery, it was soon established that many dyes and pigments could sensitize almost any type of biological system (plants, animals, cells, viruses, biologically important molecules) and result in cell damage, induction of mutations or cancer, and death.

Photodynamic Effect of Rose Bengal and Erythrosin Against Insects

The first reported use of photodynamic action against an insect target was a study of *Anopheles* and *Culex* mosquito larvae, which were shown to be susceptible to solutions of several classes of dyes in direct sunlight. The most active dyes were the halogenated fluorescein derivatives, erythrosin and rose bengal, alone and in mixture. There were no deaths reported from populations used as control for the effect of dye or light alone. A mixture of rose bengal and erythrosin was found to be the most effective, showing high larvicidal activity at a dilution of one part of dye-mixture in 1.5 million parts of water in direct sunlight. Damage to larval alimentary tract was noted.

Another study found that *Anopheles maculipennis* larvae with a series of dye solutions (10 ppm (W/V)) and exposed to sunlight were sensitive to dyes. Field tests in small ponds demonstrated that rose bengal or acridine red caused 100% mortality, and erythrosin in about 90% mortality. However, eosin and fluorescein were ineffective. The larvae of another species of *Anopheles* (*A. superpictus*) and those of *Aedes aegypti* were also similarly sensitive, whereas there was no effect on the mosquito fish (*Gambusia* sp.) that were present.

The modern era of photodynamic insecticide studies began with the report of T.P. Yoho and associates in 1971. The paucity of literature on the effects of phototoxic agents on insects, until this period, is not surprising. Light often has been a forgotten or underestimated factor in the study of insects. Even until recently little attention has been paid to its role as a parameter in the mortality of insects.

Yoho's group at West Virginia University published several investigations on the efficacy of photodynamic action against the adult house fly using primarily the halogenated series of dyes. These papers compared toxicological data with the parameters of light source and intensity, dye structure and concentration in the diet, source of light, and length of light exposure. It was observed that all house flies fed on diets containing either rhodamine (625 ppm) or erythrosin B (1,250 ppm) were killed after a 3-h exposure to light, whereas, when the dye-fed house flies were kept in the dark, no adverse effect was observed. It was also reported that the midgut epithelial cells appeared to be damaged and that the external symptoms associated with toxicity suggested an involvement with the nervous system.

Yoho and associates also studied a series of 14 food, drug and cosmetic dyes for efficacy in photodynamic toxicity to house fly adults. Nine of the 14 dyes tested produced up to 100% mortality in illuminated flies, particularly in those receiving liquid diets with a concentration as low as 0.25% dye (2,500 ppm). Lower concentrations were not tested.

The results of these investigations motivated other scientists to work on insecticidal properties of a series of common dyes. It also led to the registration of a formulation of erythrosin B under the name of "Synerid."

Practical Aspects of Erythrosin B in Insect Control

In 1980, G. D. Pimprikar and associates reported on their attempts to control house flies in a commercial caged layer house, under minimal light, using weekly applications of aqueous solutions of erythrosin B directly on the manure (about 650 mg a.i./m^2). They reported decreases of adults and larval house flies up to 90% with respect to pretreatment levels with no change in the beneficial soldier fly larval population. Their additional studies on the effects of several fluorescein derivatives in the diet on each developmental stage of the housefly revealed that the treated adults exhibited lowered fecundity, the eggs had a reduced viability, and mortality was observed in each life stage of the house fly. This experiment which was also conducted under minimal light, required a relatively large amount of dyes for 100% mortality: e.g., 0.5 g a.i./kg diet for rose bengal and 2 g a.i./kg for erythrosin B.

In 1981, T. L. Carpenter and associates reported on the role of fluorescein on enhancement of the phototoxicity of rose bengal, and some other xanthene dyes, towards *Aedes* larvae. Subsequently, a United States patent was issued covering the synergism of a nontoxic dye with a demonstrated toxic dye in both house fly and mosquito systems. Further studies resulted in an over twofold increase in the toxicity of erythrosin B against house flies.

In 1983, N. C. Respicio and J. R. Heitz reported development of resistance to erythrosin B in the house fly. While a laboratory strain developed only sixfold resistance after 40 generations, a wild strain experienced a 48-fold resistance after 32 generations of exposure to increasing levels of erythrosin B in the diet. Upon removal of the selection pressure for 20 generations, the resistance remained constant. Furthermore, the erythrosin B-resistant strain was cross-resistant to phloxin B and rose bengal, as it is to be expected since they function by same mechanism. Whereas, no cross-resistance of the resistant strain to conventional insecticides was observed.

In 1984, Primprikar and Heitz observed an unusually high insecticidal activity in *Aedes* mosquito larvae which had been illuminated after exposure to the insoluble free acid forms of the xanthene dyes. In all previous studies, the larvae had been treated with the water soluble salt forms of the dyes and the larvae consumed the dye as they ingested in the water. With the insoluble dyes they were able to filter feed on dye particles and thereby receive higher levels of these chemicals. Toxicity ratios ranged up to 2 orders of magnitude between the soluble and insoluble forms of the same compound.

A simultaneous report of Carpenter and associates showed that insoluble forms of the xanthene dyes were tenfold more effective against *Culex* mosquito larvae than the soluble forms, when used at the same dosage. They also reported that when the insoluble forms of the dyes were dispersed with a surfactant, such as sodium lauryl sulfate, the dyes were 50- to 60-fold more effective than the soluble forms. Depending on the concentrations under consideration, the increase in toxicity ranged from 26- to 229-fold for erythrosin B and 13- to 206-fold for rose bengal. Therefore, doses of free acid, dispersed formulations were in the lower ppm to upper ppb range for up to 24 h of light exposure.

In 1985, Carpenter and associates reported that a series of eight dispersants for use with the insoluble forms of the dyes were evaluated and none were toxic alone. Erythrosyin B, dispersed with sodium dodecyl sulfate, was the most toxic against *Culex* mosquito larvae. In small-scale field tests, this formulation caused significant reductions in larval and emergent adult populations of *Culex* mosquitoes at concentrations ranging from 0.25 to 8.0 ppm. Nevertheless, possible limitation of the activity in "naturally basic waters," as a result of conversion of Erythrosin B to the soluble ionized form, was suggested.

Following the studies on phototoxic activity of erythrosin B against insects, a formulation of this dye has been registered under the name of "Synerid Fly Control B." Presently, this is the only dye commercially available for insect control.

Mode of Action of Photosensitizing Dyes in Insects

Photoactive dyes were found to have numerous effects on insects (Fig. 47). Acetylcholinesterase from the black imported ant and the boll weevil was susceptible to dye-sensitized photooxidation in vitro, but levels were not depressed in insects killed by photodynamic action. It was also reported that in the American or Oriental cockroach, photodynamic action induced by rose bengal or erythrosin B caused a significant decrease in hemolymph (over 90% reduction by erythrosin B) and a large increase in the crop volume (over threefold increase in erythosin B treatment). Furthermore, photodynamic action induced by erythrosin B resulted in up to 40% reduction of hemocytes relative to controls.

Under fluoroscent light and at rose bengal treatment levels of 1–20 ppm, *Culex* larvae were

1. Conversion of sensitizer (sens) to an electronically excited state (sens*)

a) Sensitizer is either converted to a short-lived single state, i.e.

$\text{Sens} \underset{hv}{\Rightarrow} {}^1\text{sens}^*$, or

b) It undergoes further to the longer-lived triplet state, i.e.

$^1\text{Sens}^* \underset{hv}{\Rightarrow} {}^3\text{sens}^*$

2. Production of radicals or singlet oxygen ($^1O_2$)

$\text{Sens}^*\ ({}^1\text{sens}^* \text{ or } {}^3\text{sens}^*) \xrightarrow[\text{Substrate or solvent}]{} \text{Radicals (Type I Reaction)}$

$\text{Sens}^*\ ({}^1\text{sens}^* \text{ or } {}^3\text{sens}^*) \xrightarrow[\text{Moleular oxygen } (O_2)]{} {}^1O_2 \text{ (Type II Reaction)}$

3. Oxidation of vital molecules

$\text{Radicals} \xrightarrow[\text{Moleular oxygen } (O_2)]{} \text{Oxygenated products}$

$\text{Singlet oxygen } ({}^1O2) \xrightarrow[\text{Substrate}]{} \text{Oxygenated products}$

Photodynamic Action in Pest Control and Medicine, Figure 47 **A schematized version of reactions involved in the process of photodynamic action. These include (1) conversion of sensitizer to an electronically excited state, (2) production of radicals or singlet oxygen, and (3) oxidation of vital molecules. Energy (E) imparted by this excitation is related to Planck's constant (h) and the frequency of radiation (v) (see the text).**

more susceptible than *Aedes* larvae, and early instars were more susceptible than later instars. Physiological and morphological abnormalities were observed in the pupal and adult stages when the mosquito was treated during the larval period, suggesting improper chitin formation in the insect. This sometimes resulted in incomplete release of the pupal stage from the larval cuticle and of the adult stage from the pupal cuticle. Where this was observed, mortality resulted. They also observed larval-pupal intermediates similar to those found after treatment with insect growth regulators.

The abnormalities observed in insects have led to the hypothesis that these photosensitizers may have an effect on the molting hormones. There is experimental evidence that the titers of the two most prominent molting hormones in insects (e.g., α-ecdysone and β-ecdysone) are distinctly different in the erythrosin B-treated insects as compared to the control insects. According to these studies the imbalance of the molting hormone titers during the critical stages of development may contribute to the abortive molting or to the development of morphologically abnormal individuals.

Persistence of Erythrosin in Biological System

In 1981, T.E. Fairbrother and associates made a comprehensive study of the toxicological effects of erythrosin B and rose bengal on the face fly. These dyes were incorporated with manure, either by hand or by passage of the dye through cattle. When larvae developed on the manure containing either erythrosin B or rose bengal, mortality was observed at each life stage. Wing deformation in some emerging adults and incomplete removal from the puparium were also recorded.

Adults, held from emergence and illuminated with visible light, were observed to have a much higher mortality than controls, thus suggesting that dye sequestered in the insect body during development from larvae to adult was responsible for the toxicity. This is the first report of photodynamic action occurring in a life stage different from the life stage in which the dye was ingested. This was confirmed in 1982 by studies of the inhibition of growth and the photodynamic action caused by rose bengal and erythrosin B in the housefly. House flies which had consumed a nonlethal amount of dye in the larval period exhibited a considerable light-dependent toxicity in the adult stage.

Effect of Photosensitizing Dyes on Other Organisms

Although most of the photodynamic studies with the fluoroscein dyes concerned insects, and to some extent other animals, phototoxicity of eosin to chloroplasts and that of erythrosin B to the infectious third stage larvae of gastrointestinal nematodes have been recorded. Furthermore, the effect of photodynamic action on the eggs of sea urchins also has been reported. Simultaneous irradiation of eggs of sea urchins (*Paracentrotus lividus*), incubated in 0.1 mmol/l solutions of two singlet oxygen sensitizers (i.e hematoporphyrin derivative- Hpd- at 60 ppm or rose bengal- RB- at 102 ppm solutions), led to different phototoxic reactions. For example, inhibition in formation of fertilization membrane (which is required to inhibit polyspermy), shrinkage of the egg surface, appearance of many small holes in the eggs, formation of larger holes, breakage of the eggs, and finally leakage of cytoplasm.

For additional information on properties of photosensitizing dyes refer to the following section.

Photodynamic Therapy

The use of photoactive dyes as therapeutic agents (i.e., photodynamic therapy) only began in the 1960s. In 1966, Lipson reported on the practical treatment of a patient with metastatic chest wall breast cancer by a hematoporphyrin derivative. Photosensitizing dyes are currently being investigated as potential agents in the photochemotherapeutic treatment of tumors and for other medical applications. In Canada, the use of hematoporphyrin derivatives in tumor phototherapy has recently received approval for clinical use. Furthermore, second-generation photosensitizers such as phthalocyanines or benzoporphyrins that absorb in the far-red or near-infrared region are receiving increasing attention because of the ability of light of these wavelengths to penetrate tissue. Such absorption properties would permit deeper penetration of exciting light into the skin and lower doses of photosensitizer.

The laser beam (632 nm) has also been successfully used for endoscopic photodynamic therapy of gastrointenstinal neoplasms, following a 60 min infusion of the patient with hematoporphyrin (2.5–5.0 mg/kg of body weight). Furthermore, the controlled application of photosensitization has been exploited for the relief of the symptoms of some skin diseases, and therapy of different types of malignant tumors.

Viral components, including nucleic acids and lipid-rich envelopes, are potential targets for photochemical attack. Indeed, a number of photosensitizers have been able to inactivate viruses at both the DNA and the envelope levels. Nevertheless, it has been shown that enveloped viruses are significantly more sensitive (by several orders of magnitude) to photodynamic destruction than are non-enveloped viruses.

Hematoporphyrin, also known as photofrin or porphyrin, is the only photosensitizer to date to have been used extensively in the clinical treatment of a variety of malignancies. Since it is activated at a wavelength of 630–635 nm, a wavelength that is seriously decreased by hemoglobin, its antiviral activity in blood (in vivo) is expected to be reduced. Notwithstanding this fact, it has been found to inactivate a number of human viruses in tissue culture or blood: i.e., HSV (type 1 and type 2), VSV, CMV, measles, SIV, and HIV (all of which are enveloped viruses). In contrast, non-enveloped viruses have been shown to be unaffected: e.g., ECHO 21, poliovirus (P1) and adenovirus (AD12).

Because there is differential photodynamic activity of hematoporphyrin on enveloped and non-enveloped viruses, inactivation of the virus envelope is suggested. Photoactivation occurs primarily as a result of the oxidative modification of the lipid and protein components of the viral envelope. The inactivated virus is then unable to adsorb to or to penetrate into host cells, hence it cannot initiate an infection or induce the formation of viral antigens. Two other groups of photosensitizers, psoralens and hypericin, also have been found to be virucidal agents.

Extent of Penetration

Although UV, visible, or near infrared radiation could be possible energy sources for photodynamic therapy of patients, UV radiation is considered disadvantageous because of low penetration. In the course of studies on photodynamic therapy of tumors in humans, it was soon recognized that by using hematoporphyrin derivative and long wavelength light (e.g., red: above 600 nm), both greater activity and deeper tissue penetration could be achieved. While UV penetration into tissue is estimated at less than 0.1 mm, the typical penetration depth in living tissue of the red light used for photodynamic therapy ranges between 1 and 3 mm.

Mode of Action in Photodynamic Therapy

Singlet oxygen is the basis for photodynamic killing of cells for several classes of sensitizers, including xanthene dyes such as rose bengal. Although both proteins and lipids are photooxidized, proteins are generally believed to be a critical target leading to the disruption of function in cell membranes. Singlet oxygen is a genotoxic substance which can be produced in vivo, inside or outside cells causing severe damage to various biological macromolecules, even to those deeply embedded inside the cells such as DNA.

Aerobic organisms have evolved antioxidant defenses against most reactive oxygen species (e.g., superoxide dismutase, catalase, glutathione peroxidase and DNA repair enzymes, and low molecular weight agents such as α-tocopherol, β-carotene and ascorbic acid), but the antioxidation mechanism does not appear to be always effective. In this case, when active oxygen species are not adequately removed, an oxidative stress situation appears in the cell resulting in major metabolic dysfunctions. These include membrane peroxidation, rise in intracellular free calcium ions, cytoskeletal disruption and DNA damage. Singlet oxygen can mediate the oxidation of major cellular molecules. DNA, proteins and lipids are all at risk. When singlet oxygen is generated inside cells, it is very genotoxic leading to an important mutagenic effect. When singlet oxygen is produced extracellularly, it reacts with the lipids of the cellular membrane as the major target. In addition, DNA also can be attacked. Reactions leading to peroxidation of the membrane and DNA are discussed by Legrand-Poels et al. (1993).

Effect on Tumor and Non-target Tissues

Tumor destruction in photodynamic therapy is the result of the combination of direct cellular toxicity and damage to tumor microvasculature. It has long been realized that a significant proportion of photodynamic tissue destruction involves the vasculature. These phenomena appear to be caused by tissue interactions with toxic oxygen compounds which are formed when light interacts with photosensitizing agents.

The targets of photodynamic sensitizers such as hematoporphyrin are predominately the plasma membrane, mitochondria and lysosomes and, to a lesser extent, nuclear sites. Photodynamic treatment has been reported to affect transmembrane transport systems in fibroblasts, to influence lipid bilayer membranes, and to alter membrane potential in renal cells. Although nuclear aberrations, mutagenicity, micronuclei and strand breakage occur in photodynamically treated patients, the induced abnormalities may not be severe enough to cause side effects in these patients. However, there is no question that major changes occur to both tumor and surrounding normal microvasculature during and following photodynamic therapy. Changes in the endothelium, smooth muscle contraction, and increased capillary permeability have also been observed during therapy.

In addition, the oxidative stress which is mediated by intracellular generation of singlet oxygen by rose bengal photosensitization in cell culture, has been found to reactivate HIV-1 from latently infected lymphocytes and monocytes. It is a possibility that HIV-1 reactivation caused by rose bengal leads to AIDS progression by impairing the antigen presentation function or increasing infection of the adjacent T cell population of the skin, in vivo.

Cellular porphyrin distribution by fluorescence microscopy shows staining of the nuclear membrane without induction of damage. Recent experiments revealed an initial fast (within minutes) and uniform penetration of the dyes into the nuclear envelope and chromocenters. This may indicate that the matrix between the nuclear membranes is a primary target for the dyes.

Risks and Benefits

Analysis of the risks and benefits of photodynamic action is very complex, especially when the photodynamic therapy of patients suffering from malignancies, AIDS or other disorders is taken into consideration and photodynamic effects in humans such as photosensitive porphyrias (i.e., porphyrin metabolism disorders), drug photosensitivity, and photoallergies are included.

With the application of laser beam technology in endoscopic photodynamic therapy, successful treatment of certain internal cancers has been achieved (e.g., gastrointenstinal neoplasms), and experimental results from photoinactivation of viruses by hematoporphorin derivatives in cell-containing blood products also are promising. In fact, with the impressive light-mediated activity of hematoporphyrin, a new chapter in clinical trials for the treatment of HIV-infection and AIDS has been opened. Furthermore, the discovery of the second-generation photosensitizers that absorb in the far-red or near infrared region (e.g., phthalocyanines or benzoporphyrins) is promising because of the ability of these light wavelengths to penetrate tissue. Such absorption properties would permit deeper penetration of exciting light into the skin and lower doses of photosensitizer.

The simultaneous appearance of numerous reports on the success of phototoxins as insecticides also has played a great role in a growing optimism concerning the future of photodynamic agents in agriculture. This is manifested by the recent registration of erythrosin B in the U.S.A. for insect control.

Both the economic and the environmental aspects of using photodynamic pesticides, with special reference to dyes, have been studied. While some literature lists the prospects of using photodynamic dyes, others suggest the potential dangers of food, drug, and cosmetic dyes. Often they are considered to be extremely safe and pose no threat to the health or welfare of the applicator or environment in field usage, with many of them being registered as food additives. Arguments have been presented for speedy registration, requiring few label restrictions, and limited toxicological testing of the photoactive dyes.

An important reason for serious concern about the environmental threat of the photodynamic agents is the method by which their toxicity is evaluated. Since light has not been considered as a parameter, in many toxicological data which are usually presented by LD_{50} for rats or mice, the validity of such data needs to be reexamined before making a general conclusion on safety.

Because the time required for initiation of phototoxicity is very low, detoxification does not appear to prevent sublethal toxicity. Therefore, development of new strategies in the marketing of foods, drugs and cosmetics and new techniques in toxicological studies of these compounds (using light as a parameter) is indispensable. More needs to be known about the long-term effects of these materials and their terminal residues, including their use as insecticides.

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Photokinesis

Kinesis response with respect to a gradient of light.

Photoperiod

Daylength. Length of daylight during a 24-h day-night cycle.

► Diapause

Photoperiodism

Response of an organism to periodic changes in day length.

Photosynthesis

The utilization by plants of the energy provided by sunlight to split water and fix (synthesize) carbon dioxide into sugars.

Phototaxis

The taxis response of a cell or organisms toward or away from light.

Phragma (pl., phragmata)

An internally projecting structure or internal ridge in the insect body, usually an extension of the endoskeleton, but also a membrane that partitions the body.

Phragmosis

A condition in which the head or tip of the abdomen is used as a plug for the nest entrance. This behavior occurs in ants and termites, usually performed by the soldiers.

Phthiriasis

A disease of the skin resulting from an infestation of sucking lice (pediculosis).

► Human Lice

Phthiraptera

An order of ectoparasitic insects affecting mammals and birds. Considered by some to be divided into two orders, Mallophaga (chewing lice) and Siphunculata or Anoplura (sucking lice).

► Chewing and Sucking Lice

Phyletic Lines

Links drawn between present and past taxa that imply their evolutionary relationships.

Phyletic Speciation

The gradual transformation of one species into another without an increase in species number at any time within the lineage. Also called vertical evolution or speciation.

Phylogenetic Tree

A graphic representation of the evolutionary history of a group of taxa or genes.

Phylogenetics

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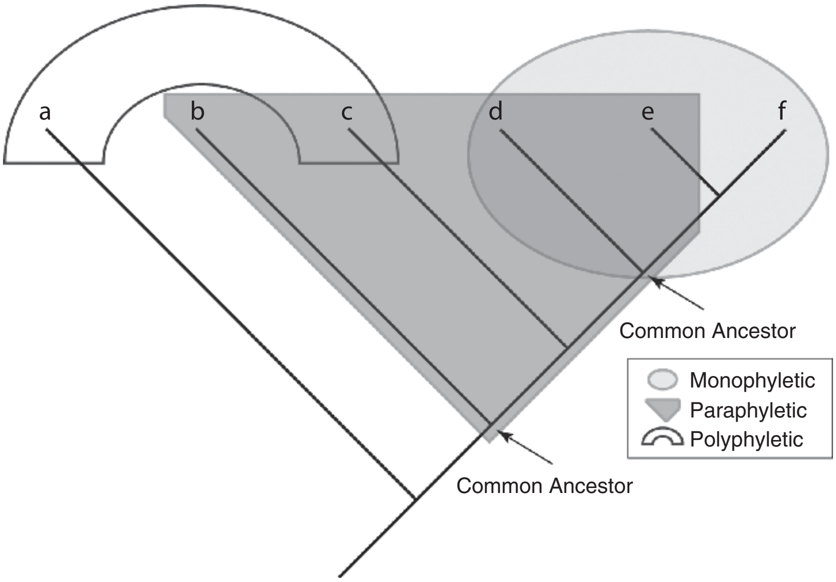
Phylogenetics is a relatively young and rapidly growing subdiscipline of the much older and larger discipline known as systematics. There are three complementary subdisciplines within systematics: taxonomy, classification, and phylogenetics. While taxonomy is used to describe the Earth's biodiversity through identifying "kinds" and placing like kinds into definable groups, based on variation (usually termed species), and classification is used to arrange these species into a hierarchical scheme of relationships (class, order, family, etc.), phylogenetics is often used to unite both taxonomy and classification by organizing the accumulated data from each species into groups representing a broader biological context. This context is usually one of evolutionary significance. One of the main purposes of phylogenetics is to unite related organisms into a natural or monophyletic group. A monophyletic group is an assemblage of organisms that includes a common ancestor and all of its descendants. Occasionally, taxa are assembled into groups that represent artificial groupings of organisms, i.e., those which are not natural. These groupings, which are called para- or polyphyletic, have fallen into disfavor as they exclude closely related taxa. A paraphyletic group contains a common ancestor but does not include all the descendants of that ancestor. A polyphyletic group does not contain the common ancestor nor all close relatives of a group of taxa. Determining whether a group is mono-, para-, or polyphyletic is done by including species of a hypothesized group in a phylogenetic analysis, which groups species based on inferences of their shared ancestry (Fig. 48). Homology is the similarity of biological structures due to shared ancestry; thus statements of homology are hypotheses about the origin and similarity of biological features among organisms. There are many forms of biological data upon which homology statements can be based, such as DNA, morphological, or behavioral data. Phylogenetics offers a rigorous framework by which multiple homology statements can be tested simultaneously, resulting in phylogenetic trees that represent patterns of relatedness, like a very large "family tree." Phylogenetics is the process by which hypotheses of evolutionary relationship (phylogeny) can be formulated and tested. A revised classification is a desired outcome of phylogenetics.

Since phylogenetics is dependant on our ability to make homology statements based on data gathered from both extant and extinct organisms, a knowledge of Earth's biodiversity is essential. Building phylogenetic trees that reflect monophyletic groups is essential to scientists researching the processes of evolution. Many insects have interesting behaviors such as flight, communication and sociality, to name only a few, that are central to understanding many of the biological processes observed among insects and that have served to shape their evolutionary history for millions of years. The phylogenetics of insects is made more interesting given that insects are the most diverse group of organisms on the planet, and as such, they have the most diverse range of morphologies, behaviors, ecological adaptations and natural histories. Organizing the diversity of



Phylogenetics, Figure 48 **An illustration of the three types of groupings: monophyletic, paraphyletic and polyphyletic. Phylogenetics seeks to identify, categorize and name only monophyletic groups. Note that there is no common ancestor for a group that is polyphyletic.**

insects into monophyletic groups within a phylogenetic framework is a major task and will be the chief focus for the field of phylogenetics for many years to come.

What Types of Data Are Used in Insect Phylogenetics?

Phylogenetics is dependent on data gathered from heritable variation that can be directly compared via homology statements. Scientists have to be sure that each character within the data set being compared is homologous across all species or kinds in the data set. For example, it would not do to compare the elytra of a beetle with the wings of a bird because beetle elytra and bird wings do not share a common origin, have special similarity or share similarity in their position, even though they are both part of the flight mechanisms for their respective organisms. Structures such as bird wings and beetle elytra share no evolutionary or developmental past and are called analogous characters. Only homologous characters should be used within a phylogenetic analysis. Traditionally, the most common type of data used within insect phylogenetic analyses is morphological data, although molecular data is fast becoming the norm among most of today's phylogenetic research. Other types of information such as behavior, ecology, physiology and developmental characters can also be used to reconstruct phylogenetic relationships.

Morphological Data

Insects have a great deal of morphological variation due to the number of ecological niches they inhabit and their diversity. Insects make use of most of the organic materials on Earth, from dung to flesh, from fungi to trees, and from mud to silk. Insects eat, produce, construct, and even culture these materials. The morphological diversity and innovation found among insects is unmatched by any other group of organisms. This astounding morphological variation is made even more impressive by the insect's ability to metamorphose. While many insects, such as grasshoppers, feed on the same diet and inhabit a similar ecological niche their whole lives, most holometabolous insects exhibit morphological changes reflective of a shift in ecological niche during the immature and adult life stages. For example, female mosquito larvae have opposed mandibles and feed mostly on detritus or micro-organisms. However, as adults their mouthparts have become modified into a serrated syringe-like structure suitable for piercing skin and extracting blood. There are also extreme shifts in the morphology of some hemimetabolous insects due to changes in ecological niches during the immature and adult life stages. For example, mayflies, dragonflies and stoneflies are aquatic during their immature stages and undergo large morphological changes in gill, eye, and skeletal morphology to become successful terrestrial adults. Many insects undergo lesser modifications of their morphology between instars (each developmental stage between moults (ecdysis) until the adult stage is reached) such as praying-mantids, true bugs, thrips, and strepsipterans. These shifts in morphology have evolved in response to factors such as food shortages, the need for protection, or life stage requirements.

Morphological data is also crucial to phylogenetic studies that seek to include insects from the fossil record since fossils (with the rare exception of some encased in amber) by definition lack DNA. Fossils also play a major role in allowing scientists to better understand the current morphological adaptations we see among related present-day taxa because they often exhibit the more primitive forms of morphological features.

Molecular Data

Today phylogenetic analyses are increasingly including molecular data for several reasons. Over the past decade, the amplification, comparison and analysis of DNA sequence data have become more straightforward, reliable, faster, cheaper, and more routine than ever. This trend will likely continue. Further, both mitochondrial and nuclear genomes are being isolated from insects to form phylogenetic hypotheses. There are, however, still challenges to using molecular data within a phylogenetic context. The software used to align sequence data (i.e., provide homology statements between nucleotides of a DNA sequence) and perform phylogenetic analyses is still inadequate for large data sets consisting of more than ~600 specimens for only a few genes. Nonetheless, molecular methods have proven to be very powerful and insightful for resolving many questions concerning insect phylogenetics.

Molecular data has also proven to be helpful when resolving relationships among species or groups of insects that have evolved unique morphological or behavioral adaptations that are difficult to homologize with existing data (see below, What is going on in insect phylogenetic studies?).

Combined Analysis or Total Evidence

It is widely accepted that a powerful approach for generating phylogenetic hypotheses is to combine large amounts of morphological and molecular data within a single analyses. This is referred to as a combined or total evidence analysis. This approach is generally preferred because it allows molecular, morphological, and any other type of data, to influence the resulting phylogenetic hypothesis in the same analysis simultaneously. This technique often produces more robust estimates of phylogenetic relationships and evolutionary hypotheses than when using only one type of data. Simply put, a total evidence analysis produces a phylogenetic hypothesis generated from the largest amount of data at hand and in which all the data contributes to the construction of the hypothesis.

What Are the Major Modern Methodologies Used in Phylogenetics?

Phylogenetic analyses result in tree diagrams called phylogenies, or simply, trees. Tree reconstruction within phylogenetics is no simple task. The number of possible trees increases dramatically as the number of taxa (individual specimens or gene sequences) included in the analysis increases (Fig. 49). The total number of possible trees for a given number of taxa (n) can be determined with the following formula:

$$\frac{(2n-3!)}{2^{n-r}(n-2)}$$

As there are so many potential trees when even a small number of taxa are included within a phylogenetic analysis (e.g., ~14 million potential trees for 12 taxa), there are multiple methods for tree reconstruction currently employed today. Modern analyses are performed almost exclusively using three major methods: Maximum Parsimony (called simply MP or parsimony) and two model based statistical approaches: Maximum Likelihood (ML) and Bayesian.

Maximum Parsimony

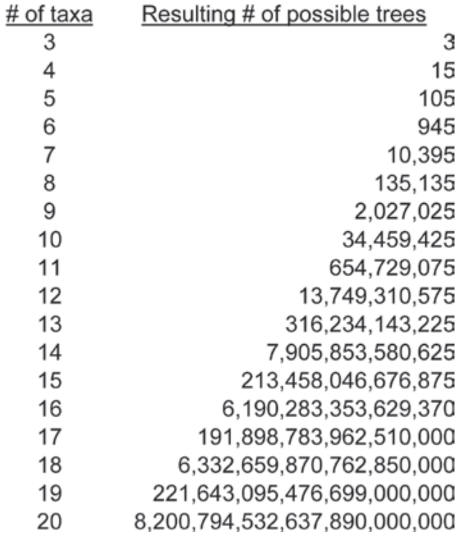
Maximum Parsimony (MP) is simplistic in its approach to phylogenetic analysis. MP finds its origins in “Occam’s Razor,” *lex parsimoniae*, which states that the explanation of a phenomenon that makes the fewest assumptions is the preferred explanation. Trees are scored such that the most parsimonious, or simplest, explanation for relationships among the taxa included in the analysis given the data is most defensible. Thus, the tree that is most parsimonious has the fewest evolutionary steps and is the favored hypothesis. This approach does not mandate that evolution always occurs in a parsimonious fashion, but rather uses the principle of parsimony to choose among competing phylogenetic hypotheses (i.e., phylogenetic trees).

MP is commonly used among entomologists, especially those using morphological data. It is also useful for molecular sequence data and generally gives very similar results to those generated by both maximum likelihood and Bayesian approaches. The most often cited weakness of MP is that of "long branch attraction" when using molecular data. Because there are only four possible nucleotides at any given site along a DNA sequence, the result is an increased probability of two or more taxa with rapidly evolving DNA (i.e., high substitution rates) to evolve the same nucleotide at the same position. Long branch attraction takes place when at least two taxa representing rapidly evolving lineages are inferred to be closely related, due to similarities along their rapidly evolving DNA, when in fact they are not. This problem is often overcome in MP analyses by including a broader range of taxa and thus more diversity in molecular sequence data that serves to break up phylogenetic relationships that could be potentially recovered as a result of long branch attraction.

Statistical Approaches

Maximum Likelihood (ML). ML is used with molecular sequence data and is a more complex approach to tree reconstruction than MP. ML differs from MP in that an explicit model of sequence evolution is used to provide an approximation of the data's origin. In addition, because this approach is model-based, it is viewed as a parametric approach to estimating phylogenetic hypotheses. ML is seen by many systematists as a more attractive method because of its statistical foundation.

Although becoming more rapid, ML is still a slow process for large data sets. Until computer computational power catches up with the demands of imposing a complex model over large molecular data sets, MP will continue to be used. However, ML is probably used more often than parsimony for moderately sized data sets. In general, both ML and MP usually converge on the same phylogenetic relationships. Although ML outperforms MP in some respects (e.g., it is less susceptible to long branch attraction), its utility is directly linked to the ability of the model used during tree reconstruction to represent the data accurately. A model that does not accurately represent the data will bias the resulting tree.



# of taxa	Resulting # of possible trees
3	3
4	15
5	105
6	945
7	10,395
8	135,135
9	2,027,025
10	34,459,425
11	654,729,075
12	13,749,310,575
13	316,234,143,225
14	7,905,853,580,625
15	213,458,046,676,875
16	6,190,283,353,629,370
17	191,898,783,962,510,000
18	6,332,659,870,762,850,000
19	221,643,095,476,699,000,000
20	8,200,794,532,637,890,000,000

Phylogenetics, Figure 49 The approximated number of possible phylogenetic trees for 3–20 taxa (after Schuh (2000)).

Bayesian

This approach to tree reconstruction is a recent development but is becoming more and more prevalent. Bayesian phylogenetics finds its origins in Bayesian statistics, and uses *a priori* evidence (prior probabilities, although rarely used in phylogenetics) to infer a revised probability (posterior probabilities) that a phylogenetic hypothesis may be true. Bayesian analyses use the likelihood function and the same evolutionary models for DNA sequence data as ML. Just as with ML, an estimate of Bayesian phylogenetic relationships is only as good as the model used to estimate them.

Morphological models, that use the likelihood function generated from the data, can be employed in a Bayesian framework. These models have been shown to perform well with morphological data, demonstrating that simultaneous analyses of both morphological and molecular data can be performed using Bayesian as well as MP methods.

Bayesian analyses employ a Markov chain Monte Carlo process to provide a sample of trees based on their likelihood and thus can produce a credible sample of trees from which a probability of relationship among groups and taxa can be directly estimated. Many phylogeneticists view this ability, coupled with the speed of Bayesian analyses (which is generally much quicker than ML), as a great benefit.

What Is Going on in Insect Phylogenetic Studies?

Over the last decade there has been an influx of large scale phylogenetic studies undertaken by the entomological community. These efforts are producing significant phylogenetic estimates of relationship between the orders of insects and within some of the largest orders of insects (e.g., Hymenoptera, Lepidoptera, Diptera and Coleoptera). From these phylogenetic reconstructions, entomologists can directly test hypotheses of evolution and diversification across higher taxa.

Current research has led to the resolution of novel hypotheses concerning some of the more problematic relationships among the orders of Insecta. For example, (i) the relationship among the lineages of the group Dictyoptera (orders Mantodea, Isoptera and Blattodea) has long been in question and there is now an increasing amount of data that supports Isoptera as a derived group within Blattodea. Placing Isoptera within the Blattodea allows scientists to examine and answer questions concerning the evolution of gut endosymbionts that allow for the digestion of cellulose for both termites and some cockroaches. (ii) Strepsiptera has also been a problematic order as many systematists have long thought it was most closely related to Coleoptera. Currently, molecular data combined with morphological data support Strepsiptera as being most closely related to Diptera, forming the group Halteria, in reference to the halteres that both groups possess in place of well developed wings. This research has lead to the discovery that by manipulating only one gene, halteres can occur on either the meso- or metathorax. (iii) Another major dilemma within the classification of Insecta is the "Paleoptera problem." Paleoptera is composed of Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies) and both are hypothesized to represent the most primitive forms of extant winged insects. The relationship between these two primitive groups of living insects as well as to the other insect orders has long been debated as these relationships appear directly linked to the origin and evolution of insect flight. The most convincing evidence to date is based on both morphological and molecular data which indicate the Ephemeroptera as the most primitive form of extant winged insects.

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Phylogeny

The history of evolution of a group of taxa or their genes. The ordering of species and their ancestors into higher taxa based on evolutionary relationships.

► Classification

► Phyogenetics

Phylosphere

The microenvironment associated with an individual plant leaf.

Phylloxerans

Members of the family Phylloxeridae (order Hemiptera).

► Bugs

Phylloxeridae

A family of insects in the order Hemiptera. They sometimes are called phylloxerans.

► Bugs

Phylum (pl., phyla)

A unit of classification, one of the major divisions of the kingdom and containing several classes. Class Insecta generally is placed in the Phylum Arthropoda of the Kingdom Animalia, as follows:

Phylum: Arthropoda
  Subphylum Trilobita – Trilobites (these are extinct)
  Subphylum – Chelicerata
    Class Merostomata – Horseshoe crabs
    Class Arachnida – Arachnids (scorpions, spiders, ticks, mites, etc.)
    Class Pycnogonida – Sea spiders
    Subphylum Crustacea – Crustaceans (amphipods, isopods, shrimp, etc.)
  Subphylum Atelocerata
    Class Diplopoda – Millipedes
    Class Chilopoda – Centipedes
    Class Pauropoda – Pauropods
    Class Symphyla – Symphylans
    Class Entognatha – Collembolans, proturans, diplurans
    Class Insecta – Insects

In this classification system, the class Entognatha and the class Insecta are separate, though they can be placed together into the superclass Hexapoda. Formerly, however, Entognaths were commonly considered to be in Insecta. other variations also exist.

► Classification

► Orders

Physical Control

Control techniques that are based on physical properties of the environment to kill insects. examples of physical control include cold storage, heating, burning, and modification of the gaseous atmosphere in storage.

► Physical Management of Insect Pests

Physical Gill

A bubble of air that adheres to the body of aquatic insects, providing a reservoir of air or plastron.

► Tracheal System and Respiratory Gas Exchange

Physical Management of Insect Pests

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Physical control methods aim to prevent or reduce pest invasion into a crop. Various physical means function either mechanically or by affecting insects' viability or behavior. For example, insect suction devices, insect glue, and electromagnetic energy suppress insect populations. Insect exclusion screens also reduce insect density, though not through mortality. Also, color and chemicals are used to change insect behavior. Physical control methods may have some shortcomings, which must be weighed against their advantages. Physical control methods generally do not interfere with other control methods. Screens are often crucial for the implementation of Integrated Pest Management (IPM) programs. They enable the use of biological control agents as well as the use of insect pollinators. Generally, most physical control methods are environmentally safe, fit well into IPM strategies, and greatly reduce the use of chemical control.

Insect-Proof Screens and Covers

The physical exclusion of insects from a greenhouse or open field is aimed at preventing direct crop damage by insects in general, and the incidence of insect borne virus diseases in particular. Additional outcomes of the reduction of pest damage are a marked reduction in the use of pesticides, the ability to use biocontrol agents as a complementary control measure, and more effective use of insect pollinators. Pest exclusion can be obtained by applying appropriate fabrics, of mesh aperture smaller than the insects' body width, or by fitting insect repellent fabrics. These fabrics are positioned over the plants in open fields, or attached to ventilators and doorways of greenhouses. Due to the exclusion feature of the technique, the fabrics must be applied before the crop is sown or planted because they do not suppress insect populations. Screens impede ventilation and sunlight; thus, to avoid adverse effects on crops and their susceptibility to diseases, compromises are necessary in the management of air flow, light, temperature and humidity. Various types of screens and plastic covers are known to exclude insects, and the challenge for the grower is to select the type of screening best suited to solve his specific problems. Although screening is a very efficient way to prevent primary pest penetration, some pest individuals manage to enter the greenhouses, despite all efforts. These insects may build up an indoor population and cause damage. When they exceed the economic threshold level it is necessary to apply complementary control measures, such as biocontrol or environmentally safe insecticides, which would be useless without the netting. The success of pest exclusion, especially its success in preventing insect-borne viruses, has led recently to a rapid increase in the area of screened greenhouse, primarily in subtropical climate regions.

Specifications of Insect Exclusion Covers

Insect-proof covers are a general name for many types of plastic sheets and screens that prevent insects from reaching the crop. There are today several companies manufacturing or supplying screens differing from each other in aspects of mesh density and thread gauge. These variations provide differing rates of ventilation but also different rates of insect penetration. The optimal screen will be the one that maintains the indoor population density independent from the outdoor population density, but still allow ventilation. For example, if the accepted economic threshold level for tomato yellow leaf curl virus infection is 10% of virus-infected plants at the end of the season, the threshold for the whitefly population density in the greenhouse will be 1.4 whitefly/trap/day or 10 whiteflies/trap/week. As long as whitefly catches are below this threshold, growers do not need to apply complementary control means. Screens can solve the problem economically and almost by themselves. To be effective, screens must be installed prior to the pests' appearance; and all openings must be totally covered by screens, including the entrance, which needs to employ air locks. Screen maintenance (repairing rips) is of paramount importance. Furthermore, plants must be quarantined before they go into production areas, to ensure they are pest free before planting. Even with these precautions, which are not without cost, some penetration by pests may occur and require complementary pest control measures.

Microperforated and Unwoven Sheets

Agronet® and FastStart® are clear, microperforated polyethylene fabrics. Reemay® and Agryl are unwoven, polyester and polypropylene porous sheets. All are light materials (17 g/m^2) that can be applied loosely, directly over transplants or seeded soil, without the need for mechanical support. Plants easily support these materials. They are used in the open field, in early spring, as spunbonded row covers, to enhance plant growth and to increase yield. At the same time, they also proved to protect plants from insects. Reemay® is known to efficiently protect squash from *Bemisia*-borne viruses (in California), and pepper from aphid borne viruses (in Spain). FastStart® protects plants from flea beetles, root flies, moths and insect transmitted diseases (in the U.S.). Indoors, Agryl® is used to protect organically grown tomatoes from virus transmission by *Bemisia* (in Israel). High environmental temperatures may damage plant parts that are in contact with the fabrics.

Woven Screens (Whitefly Exclusion Screens)

The conventionally woven "Whitefly Exclusion Screens" – generally known as 50-Mesh®, Anti Whitefly®, or AntiVirus®, and by many other commercial names – are produced from plain, woven, white plastic yarns. These screens are made of yarns 210–230 μm thick; 24–28 yarns/in. in warp (about 10/cm), and 54–56 yarns/in. (about 20/cm) in weft, resulting in slots of rectangular shape. The limiting factor for blocking the whiteflies is the smaller width of the slot, approximately 240 μm. Insects' ability to pass through a barrier cannot be predicted solely from thoracic width and hole size. Screens are three-dimensional fabrics with a specific hole geometry, which is an important element in insect exclusion. The blocking efficacy of any screen must be tested in laboratory and/or field trials. The elongated shape of the slot improves air and light passage. However, elongating the slot more will enable the threads to slide, and whiteflies to penetrate. These screens, though developed primarily to block penetration by *Bemisia* whitefly, also exclude all insects larger than *Bemisia*, e.g., moths, beetles, leafminers, aphids, plant hoppers, and psyllids; thus they also prevent epidemics of aphid-borne viruses.

Knitted Shade Screens

The mesh of knitted screens is defined by the percentage of shade (e.g., 30, 40 and 50%) that they produce. Because of irregularity in the shape of the holes, whiteflies are not excluded. Reducing the size of the screen holes until they are capable of blocking whiteflies reduces ventilation to an impractical level. However, insects bigger than whiteflies, and birds, might well be excluded.

Knitted-Woven Screen

A new type of plastic screen (SuperNet®) is under development. It is produced by a combination of knitting and weaving. This technique produces a screening with slots almost three times longer than those of the commercial woven screen, while keeping the width of the slot smaller than whitefly body size. This screen possesses high blockage capacity for whiteflies, similar to that of conventional woven screens, but with improved ventilation.

Thrips Exclusion

Thrips are the smallest of common insect pests, with a body width of only 245 μm. They move freely through whitefly-proof woven screens. However, thrips are strongly affected by color. As a result, a high proportion of the thrips population (50%) is excluded in the field, due to the optical features of the screen's material. To improve this still-insufficient rate of exclusion, a very fine mesh screen is needed (Bugbed-12®, NoThrips®), but this hampers ventilation too much. Nevertheless, a loose shading screen of aluminum color, through which even whiteflies penetrate freely, reduces thrips penetration by 55%, contrary to a screen, similar in structure but white in color, which attracts many thrips (similarly to a white mulch).

Greenhouse Ventilation, Insect Invasion and Screens

The use of insect-proof screens reduces natural ventilation, which may in turn increase temperature and air humidity to harmful levels. This is even more likely if the greenhouse area exceeds about 1,000 m^2. In this case, natural ventilation may become insufficient, because the area of the side-openings becomes proportionately too small for the greenhouse area. Consequently, natural ventilation becomes ineffective. Forced ventilation may minimize these harmful effects, but the type of ventilation system strongly affects the influx of insects into the greenhouse. The use of vents that exhaust air from the greenhouse causes underpressure, and many insects are sucked into the structure. Alternatively, overpressure, induced by actively pushing air into the greenhouse through an insect-proof filter, reduces the influx of insect pests significantly even in unscreened greenhouses. In large greenhouses (greater than 1,000 m^2) natural roof ventilation is crucial. Obviously, the roof openings must also be protected by an appropriate insect exclusion screen.

Insect Suction Devices

Efficient removal of certain flying and non-flying insects (e.g., aphids, Colorado potato beetles, leafminers, and whiteflies) is possible with modern vacuuming machinery. Vacuum treatments, applied either prophylactically or whenever the insect population exceeds a certain threshold level, reduce populations markedly. One of many examples is the Biovac, a tractor-propelled vacuum device that can be used to control tarnished plant bug populations in strawberry crops. Field trials have demonstrated the additional benefits of enhanced pollen dispersal in strawberries coupled with no reduction in beneficial honey bee pollinators (which are able to fly out of the path of the vacuum machine). Greenhouses present unique problems due to their physical structure, but special equipment could be developed, with vacuum machines running automatically on overhead tracks. Vacuum devices are completely compatible with all forms of pest control, and can even be used in biological control by reducing pest levels before releases of natural enemies.

Insect Glue (Polybutene)

"Insect glues," e.g., polybutenes, are synthetic hydrocarbon polymers. Glue viscosity is proportional to chain length; the longer the chain, the higher the viscosity. Viscosity ranges from 0.3, a liquid with little tackiness, to 600, a very viscous grease-like material with a high degree of tackiness. "Thripstick" is a commercial mixture consisting of polybutene, an emulsifying agent, an insecticide, and water. It is sprayed under greenhouse crops, either on the floor covering or the soil. It does not affect natural enemies. It has been used successfully to control two typical soil-pupating insects: thrips and leafminer flies.

Electromagnetic Energy

The effect of electromagnetic energy on organisms is incompletely understood, although in general, longer wavelengths produce heating effects and shorter wavelength radiation produces chemical effects, including ionization of the absorbing media.

Longwaves: Radio Frequencies (RF) and Infrared (IR)

The use of RF for pest control has been frequently considered, mainly in grains, foodstuffs, and wood.

RF energy was found to be effective against some moth larvae, e.g., the pink bollworm in cotton seeds. Still, no practical large-scale applications have been yet developed. It appears that major improvements in efficiency of RF treatments are necessary for the method to become practical. Potential uses of IR for insect control involve two generally different concepts. One concept is the use of radiation directly applied to the insects or to the infested material. The other concept is based on the insect's suspected ability to sense infrared radiation and man's ingenuity in employing this knowledge in some way to achieve control, e.g., by attracting specific insects to IR lured traps for monitoring and control purposes.

Ultraviolet (UV) Radiation

Insects (e.g., aphids, whiteflies and honey bees) are sensitive to much shorter wavelengths of light than man, and may visualize the part reaching into the UV portion of the spectrum. The responsive region for insects lies, generally, between 700 nm and about 253 nm. Insects respond to visible and UV radiation in many ways, physiologically and behaviorally. The insects may be affected by the quality, intensity, and duration of light, either directly or indirectly through the host-plant. One aspect of major interest for control is that of phototaxis, movement toward or away from light. The effect of UV radiation on insects' photoperiod, diapause, and sterilization are also of interest. Investigations on insect control with UV radiation have taken two approaches: (i) the use of low-level illumination to manipulate attractive or behavioral responses, and (ii) the use of high intensity irradiation that produces adverse physiological responses. UV (black light) lured traps are used to monitor noctuid insects. UV-absorbing plastic sheets, used as a greenhouse roof cover, reduce to some extent the immigration of whiteflies, probably due to a retarding effect of their UV reflection features. Exposure of newly emerged virgin adults of *Bemisia* for 15 min to the radiation of a "Hanovia model II" ultraviolet lamp, causes complete sterilization of the males and partial sterilization of the females. Sterilization of both male and female adults can also be induced by irradiation of pupae during the last day before emergence, whereas fecundity of females is not significantly affected.

Gamma Irradiation: A Postharvest Treatment

Whiteflies, leafminer flies, and thrips are considered "quarantine pests," even at numbers far below the conventional economic threshold. Gamma irradiation, originating from 60Co, is used with doses of 2.5–200 krad/h (25–2,000 GY/h). For example, 200 krad are lethal to eggs and all immature stages of the leafminer *Liriomyza trifolii* on bean seedlings. At doses of 75 krad or less larvae survive to pupate, but do not give rise to adults. Larval and pupal radiosensitivity decrease with increasing age. Eggs and prepupae are more susceptible to radiation than other stages. Very few flies emerge from eggs or first instar larvae irradiated by 4–5 krad, and those that do are all impaired and die within 24 h. Doses of 20 krad kill eggs and all larval stages of *Bemisia* on cotton seedlings. *Spodoptera littoralis* eggs in chrysanthemum flowers are killed by a dose of 50 krad, and neonate larvae by 125 krad. Consequently, the higher dose is suitable to eliminate the pest in flowers for export.

Air Ion Stimulation

In one study, an air ion generator-emitter complex, installed above tomato plants grown in a commercial soilless culture, caused a marked decrease in greenhouse whitefly infestation and no chemical treatment was needed. When the air ion treatment was halted for 10 days whiteflies appeared. When the air ion generator was reactivated, there was a prompt reduction in whitefly activity. It appears that negative air ions diminish whitefly activity and prevent their population growth.

Visible Light

Attractive Colors

Color lured traps are an efficient monitoring device. Yellow sticky traps are used for monitoring a insects such as whiteflies, aphids, thrips, and various flies (e.g., leafminer flies, fungus flies, etc.). Blue sticky traps are more specific, attracting mainly flower-infesting insects such as thrips and the flower chafer, *Epicometis squalida*. The highly significant correlation between the number of trapped whiteflies and the number of tomato yellow leaf curl virus infected plants turns the traps into a very helpful monitoring device for control decision making.

Ground Colors and Whitefly Trapping

Ground colors affect the number of whiteflies trapped by yellow sticky traps. The highest numbers are attracted to traps placed on bare soil (100%). Black, white, and glittering transparent plastic mulches, white and aluminum colored insect screens, kaolin sprayed whitened soil, all reduce the insect catches. In the following decreasing order from black to the various white and aluminum colored backgrounds. Glittering transparent plastic and Kaolin sprayed soil are the most repellent backgrounds. This indicates the importance of reflective light when mulching is selected as a mean of control, or when traps are exposed for monitoring purpose.

The number of trapped thrips is also strongly affected by background colors. Aluminum colored backgrounds, commercial white-appearing whitefly exclusion screens, or transparent plastic sheets, significantly reduce the numbers of alighting thrips. This may explain the relatively scarce appearance of thrips in structures covered by the commercially used whitefly exclusion screens. Conclusively, thrips are affected not only by the screen mesh but also by its color. Thus, the population can be reduced drastically by using a proper combination of mesh and color screen.

Mass Trapping

Attempts to control greenhouse whitefly populations through mass trappings in greenhouses give controversial results. Some claim success while others do not, since many whiteflies are found on the plants despite the fact that many are caught on yellow sticky strips.

Colored Screens

The incidence of aphid-borne virus infection in paprika is reduced significantly by using a white screen, even when the holes were larger than aphids and the screens are not a mechanical barrier. Attempts to increase screen holes, by combining the mechanical effect of the screen with a behavioral effect of colors to exclude *Bemisia tabaci*, turn out to be insufficient. Although whiteflies react to colors, it seems that the crucial restricting mechanism of screens is mechanical rather than behavioral. The behavior of the western flower thrips is more affected by colors.

Mulches

The mode of action of mulches is not fully understood. White mulch attracts thrips to the crop, aluminum colored mulch repels them, and yellow mulch delays tomato infection by tomato yellow leaf curl virus vectored by *Bemisia tabaci*. Before using mulches their effects must be carefully investigated for each circumstance.

Whitewashes

Whitewashes are white suspensions which contain 2.5–6% Zn. They are used as repellents inert reflective materials like Ca, and various adjuvant like stickers and spreaders. They are sprayed directly onto the crop's leaves to make them white. Whitewash increases potato leaf reflectivity in the visible spectrum by 130–250%, and markedly reduces the overall number of aphids landing in whitewash-treated plots. However, different aphid species respond differently; *Myzus persicae* (Sulzer) and *Aphis fabae* Scopoli are repelled, whereas *A. gossypii* Glover is attracted to whitewash-treated pots. A water solution of Kaolin reduces remarkably both the alighting and the development of *Bemisia*, on melons and zucchini plants.

Photoperiod

Many physiological processes depend on the length of the light period. Under long day conditions, whitefly development is quicker, the progenies' body size is larger and the females lay more eggs. Sex ratio is not affected by the length of the day. Finally, the population growth rate is enhanced under long day conditions. Adult emergence time is often synchronized by the diurnal rhythm under which the immature stages had developed. Many insects survive hard living conditions by diapausing (during wintering) or aestivating during summer. In most insects, the length of the day regulates the initiation of diapause or aestivation, and its end. By artificially changing the photoperiod, the process can be disrupted and the insects die in the course of the season.

Chemically Induced Behavior Modifiers

Chemically induced behavior modifications are a well-known phenomenon in nature in general, and in insects in particular. Formulations based on safe active ingredients can act both as repellents and as physical poisons. Nontoxic, or safe active ingredients, such as behavior modifiers, repellents, knockdown agents, and physical poisons, are used to protect people and their animals, and can be used to protect crop plants. However, many of those compounds cannot yet be applied to foliage due to the phytotoxicity of their chemicals, emulsifiers, or other necessary additives. Some soaps and vegetable oils (e.g., sunflower, soybean, pea nuts, and ricinusoil) and many more chemicals are included in this group of insect behavior modifiers.

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Phytoecdysones

Ecdysone-like chemicals found in plants that affect the growth and development of insects, providing a basis for resistance of the plants to insect herbivory.

Phytophage

An organism that feeds on plant tissue (= herbivore).

Phytophagous

Feeding on plants or plant products.

Phytophagy

Feeding on plants (= herbivory). Arthropods feeding on plants are said to be phytophagous (phytophages) or herbivorous, though herbivory can be more narrowly defined as feeding on herbage, which consists of grass and other low-growing plants, not trees.

Phytophagy is one of the most common ways of living displayed by insects. Just under half of all insect species feed on plants, with the balance being either predatory or parasitic (feeding on other insects), or saprophagous (feeding on decaying material). The taxa feeding on plants tend to be among the more modern orders and contain the most species. Most evolved in response to the increased availability of modern plants (Spermatophyta), and include the orders Hemiptera, Thysanoptera, Lepidoptera, Coleoptera, Hymenoptera, and Diptera.

► Food Habits of Insects
► Allelochemicals
► Plant Secondary Compounds and Phytophagous Insects
► Graminivory
► Granivory
► Folivory
► Herbivory

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Phytosanitary Procedure

Officially prescribed methods for performing inspections, surveys, tests, or treatments in connection with regulated pests.

► Regulatory Entomology
► Sampling Arthropods

Phytosanitary Regulation

Official rules to prevent the introduction and spread of pests by regulating production, movement, or presence of commodities or other articles or personnel. This is normally enforced by establishment of phytosanitary procedures, and certification procedures.

► Regulatory Entomology

Phytoseiid Mites (Acari: Phytoseiidae)

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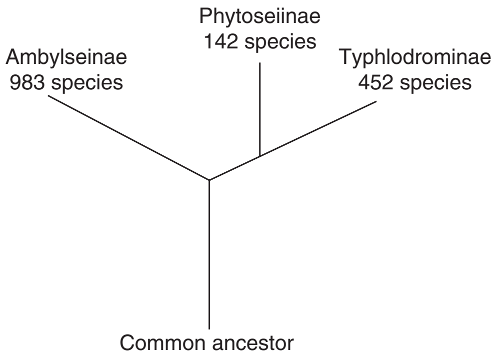
The family Phytoseiidae consists of approximately 1,700 species of small mites (200–500 µ) mostly predatory, free-living, terrestrial, and known throughout the world, except the Antarctica. They belong to the order Acari, suborder Mesostigmata, Family Phytoseiidae, subfamilies Amblyseiinae, Phytoseiinae, and Typhlodrominae (Fig. 50). The life cycle consists of the egg, larva, protonymph, deutonymph and adult. They are found on many plant species, soil, and debris. Published accounts of food sources include pollen, fungi, nematodes, mites, scale insects, whiteflies, and other small arthropods.

They have attracted attention due to their role in the biological control of small arthropods and are included in some integrated pest management programs to reduce the need of pesticides. Some of the species that are mass-reared and sold for use in biological control programs are: *Phytoseiulus persimilis* Athias-Henriot is predaceous on spider mites world wide; *Metaseilus occidentalis* (Nesbitt) is predatory on spider mites on apples, grapes, peaches and almonds in California, but is less effective on the genera *Panonychus*, *Bryobia*, and *Eotetranychus*; *Typhlodromus pyri* Scheuten is predatory on the twospotted spider mite, *Tetranychus urticae* (Koch) world wide and the European red mite, *Panonychus ulmi* (Koch) in Europe and apples in New Zealand; *Neoseiulus alpinus* (Schweizer) is an effective predator of the cyclamen mite on strawberries in Florida; *Euseius hibisci* (Chant) is considered to be an effective predator of the sixspotted mite, *Eotetranychus sexmaculatus* (Riley) in California.

Classification

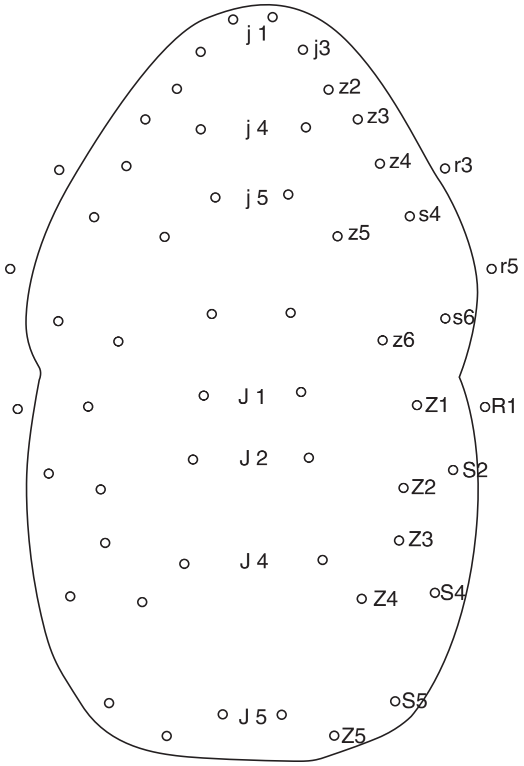
The evolution in the Phytoseiidae has been marked by the loss of many of the idiosomal setae as shown in the schematic view of a phytoseiid mite (Fig. 51). Three subfamilies are recognized by the absence of z3 and s6 in the Amblyseiinae Muma as shown in *Amblyseius mazatlanus* Denmark and Muma (Fig. 52), either or both setae z3 and s6 present and setae Z1, S2, S4, and S5 absent in the Phytoseiinae Berlese as shown in *Phytoseius chanti* Denmark (Fig. 53), and one of the setae Z1, S2, S4, and S5 present in Typhlodrominae Chant and McMurtry as shown in *Typhlodromus swirskii* Denmark (Fig. 54). There have been many attempts to classify the phytoseiids as shown in the suprageneric classification of the Phytoseiidae by various taxonomists (see Table 12).



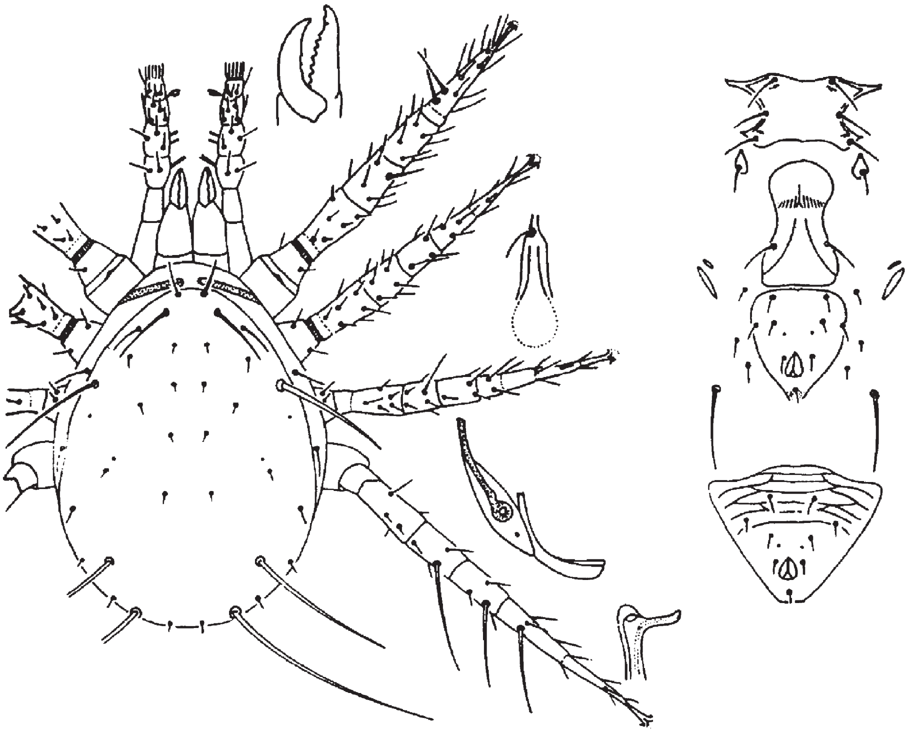
Phytoseiid Mites (Acari: Phytoseiidae), Figure 50 **Probably phylogenetic relationships of the Amblyseiinae, Phytoseiinae, and Typhlodrominae (after Chant and McMurtry).**

Ecology

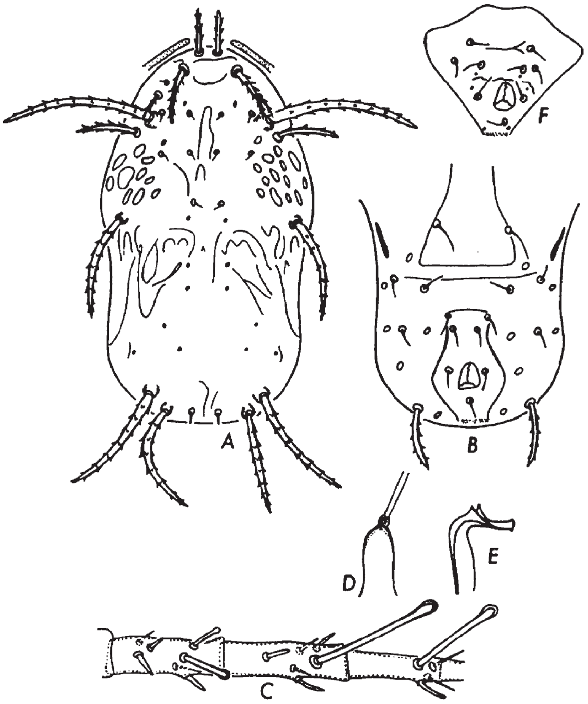
The important role that the phytoseiids play in the ecology of agriculture crops and ornamental



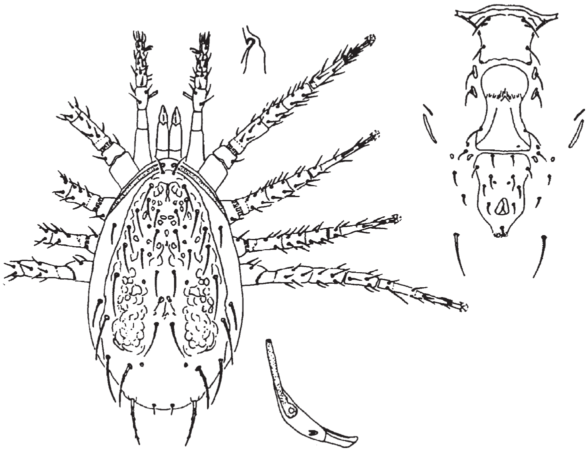
Phytoseiid Mites (Acari: Phytoseiidae), Figure 51 **Schematic view of a hypothetical adult phytoseiid mite showing the 27 pairs of dorsal setae known to occur in the family (after Chant and Yoshida-Shaul).**



Phytoseiid Mites (Acari: Phytoseiidae), Figure 52 Diagram of *Amblyseius mazatlanus* Denmark and Muma, an example of the subfamily Amblyseiinae.



Phytoseiid Mites (Acari: Phytoseiidae), Figure 53 Diagram of *Phytoseius chanti* Denmark, an example of the subfamily Phytoseiinae.



Phytoseiid Mites (Acari: Phytoseiidae), Figure 54 Diagram of *Typhlodromus swirskii* Denmark, and example of subfamily Typhlodrominae (Cydnodromellinae).

plants is poorly understood because the biology is known only for a few species. Phytophagous mites are involved in losses to agricultural, medicinal, forestry textile, fruit, ornamental and forage crops. While the availability and use of pesticides in

Phytoseiid Mites (Acari: Phytoseiidae), Table 12 Various approaches to suprageneric classification of the Phytoseiidae

Berlese[a]	Vitzhum[b]	Baker and Wharton[c]	Karg[d]
Family Laelapidae	Family Laelapidae	Family Phytoseiideae	Family Typhlodromidae
Tribe *Phytoseiini*	Subfamily Phytoseiinae	Subfamily Phytoseiinae	
		Subfamily Podocinae[e]	
Muma[f]	Hirschman[g]	Chant[h]	Karg[i]
Family Phytoseiidae	Family Gamasidae	Family Phytoseiidae	Family Typhlodromidae
Subfamily Phytoseiinae		Subfamily Phytoseiinae	Subfamily Phytoseiinae
Subfamily Macroseiinae		Subfamily Otopheidomeninae[e]	Subfamily Otopheidomeninae[e]
Subfamily Amblyseiinae			Subfamily Blattisociinae[e]
Subfamily Aceodrominae[e]			
Muma[j]	Wainstein[k]	Chaudhri[1]	Aruntunjan[m]
Family Phytoseiidae	Family Phytoseiidae	Family Phytoseiidae	Family Phytoseiidae
		Subfamily Gnoriminae	Tribe Amblyseiini
Subfamily Macroseiinae	Subfamily Phytoseiinae		Tribe Phytoseiini
Subfamily Amblyseiinae	Subfamily Macroseiinae		Tribe Typhlodromini
Subfamily Phytoseiinae	Subfamily Treatiinae[e]		Tribe Macroseiini
	Subfamily Evansoseiinae		Tribe Iphiseiini
	Subfamily Gigagnathinae		
Krantz[n]	Karg[o]	Chant & McMurtry[p]	Kolodochka[q]
Superfamily Phytoseioidea	Family Phytoseiidae	Family Phytoseiidae	Family Phytoseiidae
Family Phytoseiidae	Subfamily Phytoseiinae	Subfamily Amblyseiinae	Subfamily Phytoseiinae
Family Otopheidomenidae[e]	Subfamily Blattisociinae[e]	Subfamily Phytoseiinae	Subfamily Cydnodromellinae
Family Ameroseiidae[e]	Subfamily Macroseiinae	Subfamily Typhlodrominae	Tribe Amblyseiini

Phytoseiid Mites (Acari: Phytoseiidae), Table 12 Various approaches to suprageneric classification of the Phytoseiidae (Continued)

Berlese[a]	Vitzhum[b]	Baker and Wharton[c]	Karg[d]
Family Podocinidae[e]	Subfamily Treatiinae[e]		Tribe Kampimodromini
Family Epicriidae[e]			Tribe Phytoseiini
			Tribe Typhlodromini
			Tribe Seiulini
			Tribe Paraseiulini
			Tribe Anthoseiini

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agriculture now is essential, alternative control strategies of mites must be developed. The cost of pesticides, the development of pesticide resistance and sustaining competitive food exports to foreign markets dictate the need for new tactics of control. Students with an interest in Phytoseiidae could make a meaningful contribution by researching the biology of some of the species that are routinely collected on fruit and/or vegetable crops. IPM programs can always use additional predators to help reduce pest problems.

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Phytotelmata

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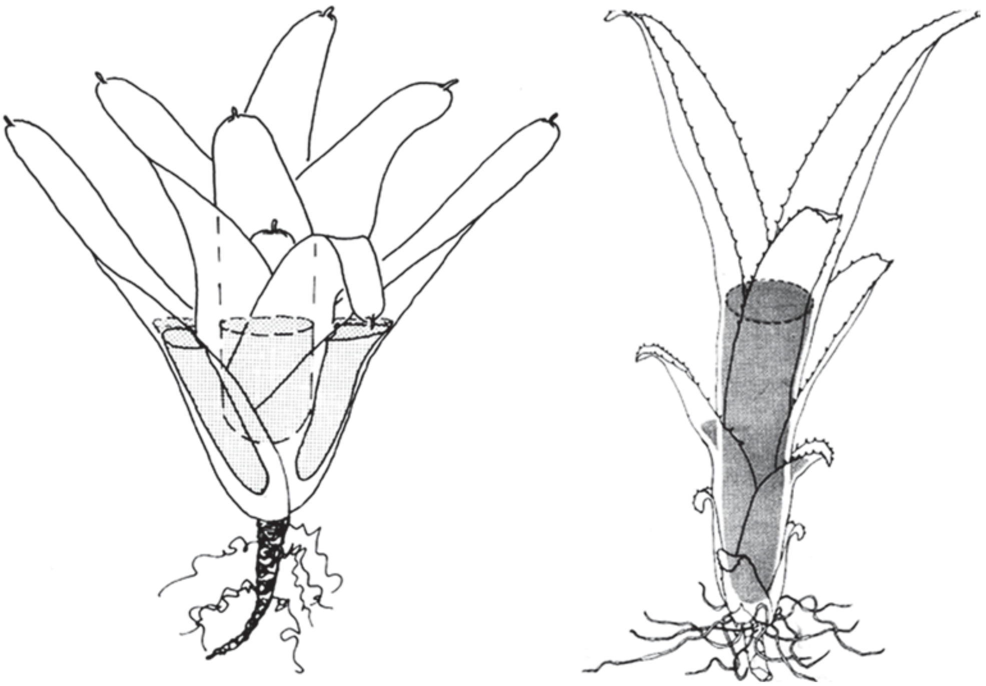
Phytotelmata are pools of water impounded by terrestrial plants. The structures that impound them are modified leaves, leaf axils, flowers, perforated internodes of plants that have internodes (such as bamboos), rot-holes in tree trunks or branches (henceforth called treeholes), open fruits, and fallen leaves. This expression, derived from the Greek words for plant and pool, was coined by Varga (1928) who wrote in German, with a companion paper in Hungarian. Maguire (1971) popularized its acceptance into English. The plural is phytotelmata (correctly pronounced phyto.TELM. ata, where the capital letters indicate location of the stressed syllable), in keeping with other plural words ending in -ata in Greek such as stemmata and stomata. The singular is phytotelma (compare with soma, stemma and stoma). The singular has been further Anglicized to phytotelm, which serves as a noun and as an adjective.

Phytotelmata formed by leaves, flowers and internodes of living plants are found in members of at least 29 plant families, mostly monocotyledons. They are Agavaceae, Amaryllidaceae, Araceae, Bromeliaceae, Campanulaceae, Cannaceae, Cephalotaceae, Commelinaceae, Compositae, Cyperaceae, Dipsacaceae, Eriocaulaceae, Euphorbiaceae, Gesneriaceae, Gramineae, Heliconiaceae, Hanguaceae, Liliaceae, Marantaceae, Musaceae, Nepenthaceae, Palmae, Pandanaceae, Rafflesiaceae, Sarraceniaceae, Strelitziaceae, Typhaceae, Umbelliferae, and Zingiberaceae. A list of plant families providing fruits or fallen leaves that form phytotelmata has not been compiled, but would be long. Treeholes are formed in just about any plant family containing hardwood trees.

Some of the plants that form phytotelmata are carnivorous. The pitcher plant families (Cephalotaceae, Nepenthaceae, and Sarraceniaceae) are not closely related to one another. Pitcher plants have modified leaves that trap and digest terrestrial arthropods as a source of nutrients for the plant. Despite the digestive fluids produced, specialist aquatic arthropods (mites and insect larvae) dwell in the pitchers of some species of *Sarracenia* (North America) and *Nepenthes* (southeast Asia and Madagascar). Carnivory is also displayed by some members of two genera of bromeliads, *Catopsis* and *Brocchinia*, although because there is no evidence of plant-produced digestive fluids, these plants have been dubbed "proto-carnivorous" by purists. In them, prey organisms are broken down by autolysis and then the products became available for uptake by the plant. Specialist aquatic insect larvae dwell in the water-impounding leaf axils of these bromeliads (Fig. 55).



Phytodelmata, Figure 55 **Figures show how the architecture of two bromeliads affects distribution of phytotelmata: left, *Billbergia pyramidalis*, right, *Aechmea nudicaulis*.**

Bromeliads are a family (Bromeliaceae) of monocotyledons with about 2,500 described species. Almost all of them are native to the neotropics. They include many species whose growth form impounds water and many that do not. Phytotelmata held by water-impounding species range from small bodies of water in several to many leaf axils (typified by some plants of the genera *Tillandsia* and *Guzmania*), or the formation of a large central tank formed by a few leaves (typified by some plants of the genera *Aechmea* and *Neoregelia*). Very many bromeliad species are epiphytic whereas others grow on the ground. None of the epiphytic species is believed to be parasitic on trees. Instead, the roots serve only as holdfasts, and water and nutrients are absorbed through pores on the leaves from the impounded water. Wet neotropical forests may support dense populations of such epiphytic bromeliads which have been likened to "aquaria in the treetops." Some bromeliads that grow on the ground dwell on rock surfaces, some in rather arid habitats and others in swamps, and in these the roots may absorb nutrients. Some of the ground-dwelling bromeliads provide phytotelmata. One species of one ground-dwelling genus (*Ananas comosus*) is an important crop plant (pineapple). Many genera, species, and hybrids are grown as ornamental plants; although many of these are epiphytic in nature, horticulturists have learned how by use of well-drained media, most may be grown in pots. The food-chains in bromeliad phytotelmata are of two basic kinds. In the phytotelmata provided by epiphytic bromeliads, rainwater falling through tree canopies is there enriched by leachates (to form throughfall), and is impounded by the plants together with debris (leaves, twigs, and seeds) of the trees. The plant obtains its nutrients from the impounded water. Various organisms inhabit the impounded water. In the phytotelmata provided by ground-dwelling bromeliads, debris trapped tends to be sparser (for lack of a tree canopy overhead), algae tend to grow in the water, and these algae form the basis of a food chain. A third kind of food chain is formed in those few bromeliads that grow in sun-exposed bromeliads and have developed carnivorous habits.

Heliconia is a genus of some 200 + species distributed in the neotropics and in some Pacific islands. It is now placed in the family Heliconiaceae, although in the past it has been variously assigned to Musaceae and Strelitziaceae. Floral spikes are pendent in some species, upright in others. Flower bracts in upright flowers may hold from a few drops to about 90 ml of water, depending upon species. Flowers emerge through this water and perhaps are thus protected to some extend from herbivory by it. At all events, the presence of water seems important to some species because they do not rely totally upon rainfall to replenish the water, but are able to pump water into the bracts. After flower fertilization, which is believed to be performed by hummingbirds or bats, the flower petals decompose in this water. The flowers are the basis of a food chain that nourishes various invertebrate animals. The first invertebrates to invade are specialist aquatic insect larvae. As the contents of each bract age, and as bract walls are damaged by vertebrate animals, the water level in the bract declines, and the bract risks invasion by semi-aquatic or even non-aquatic insects. However, the seed walls are extremely hard and thus very resistant to attack by insects. Each seed is enclosed within a fleshy, typically blue, pericarp, which doubtless makes it attractive to vertebrate animals and serves to disperse the seeds. During the flowering season, each floral spike at any time typically presents a succession, from youngest, unopened bracts at the apex, to older bracts with formed seeds.

It is not clear that other plants that impound water in leaf axils or floral parts use the water in any way. Most of these plants are monocotyledons. Fallen leaves may provide ephemeral, nutrient-poor phytotelmata during rainy seasons. Fruit husks may provide nutrient-richer phytotelmata. One example of the latter is the husks of cacao, which are usually left in piles in cacao plantations after harvest.

Treeholes provide phytotelmata in all but one continent. Those in an appropriate position in a tree trunk or large branch may be filled by stemflow. Part of the rainfall striking a tree canopy falls through it (after enrichment) as throughfall. Another part runs down branches and trunks, picking up leached materials and debris, as stemflow. Dead leaves and other debris from the canopy above may be blown into well-placed treeholes. All these materials decomposing inside treeholes provide a nutrient soup, which typically is not wasted by invertebrate animals. Some trees whose stem gives rise aboveground to roots, form bark-lined basal treeholes, which may likewise impound water. Not all treeholes impound water, not just because they are not in an appropriate position to collect stemflow, but because they have more than one opening, and leak. Some treeholes rarely receive stemflow and may be dry or almost so for months of each year. Rainfall fluxes are as important to the inhabitants of treehole phytotelmata as they are to the inhabitants of bromeliad phytotelmata.

Bamboos provide phytotelmata by one of two methods. If the stem is snapped or cut, the standing part, whose lower limit is marked by a node, can accumulate rainwater and debris. In some tropical countries, however, Coleoptera may make a small lateral hole into an internode, and this may accumulate water by stemflow. This small hole may limit access by flying insects, but some insects have adapted to injecting their eggs, giving rise to aquatic larvae, through it. The inner lining of the internode provides some nutrients.

The phytotelmata provide habitats for various aquatic invertebrates, including insects; these aquatic organisms and their habitat are of main concern in this article as "phytotelmatous." However, the plant structures around the phytotelmata provide habitat for some non-aquatic invertebrates that interact as predators with the aquatic fauna, much as do banks of ponds and streams. Other invertebrates (including insects) that dwell around the edges of phytotelmata, but that do not interact with the aquatic organisms, are numerous, but cannot be construed as part of the phytotelm fauna. Thus, lepidopterous larvae that feed on decomposing materials in non-water-holding outer leaf axils of bromeliads are not "phytotelmatous," nor are cockroaches nor ants. A few vertebrate animals, mainly frogs, have evolved to become specialist inhabitants of bromeliad phytotelmata or treeholes, laying their eggs nowhere else. But almost all phytotelm specialists are invertebrates.

Specialist inhabitants of phytotelmata typically do not harm the plant hosts. Some appear to be mutualists. In bromeliads, invertebrates (and bacteria and fungi) break down debris and may make it more easily taken up as nutrients by the leaves. Algae growing in sun-exposed bromeliad phytotelmata may perhaps compete with the plant host for nutrients, but the action of chironomid larvae is to feed on the algae, thus benefiting the host in two ways. In Heliconia bracts, it does not matter that decomposing petals are eaten by syrphid larvae after fertilization of the flowers has occurred. It does not matter that inner walls of bracts are scraped by hispine chrysomelid larvae once the seeds have formed.

Regulation of populations of invertebrates in phytotelmata takes several forms. Rainfall fluxes are, of course, of paramount importance in almost all, for the phytotelmata would not exist without rainfall. Rainfall, in the form of throughfall and stemflow, is also important for the provision of many nutrients in many phytotelmata. With water and nutrients and detritus that form the basis of the food chains, the next level of most food webs consists of saprovores (that feed on detritus) or, in phytotelmata that support algal growth, of herbivores (that feed on algae). Then, if the web is complex enough, come one or two levels of predators. Population regulation of the saprovores is brought about either by competition for resources, or by predation. It is of course the organisms that are lower in the food web (chain, pyramid) that are the most abundant.

Invertebrate animals that occupy at least some phytotelmata include rotifers, aquatic oligochaete worms, crustaceans (ostracods, copepods, and decapods), aquatic mites, and representatives of some orders of insects. Aquatic insect larvae are best represented in diversity and numbers of individuals by Diptera. For example, over 200 species of Culicidae are known from bromeliad phytotelmata alone. Culicidae are reported from all the other groups of phytotelmata, from pitcher plants through bamboo internodes to Heliconia floral bracts and fruit husks and fallen leaves. But Ceratopogonidae, Chironomidae, Psychodidae, Richardiidae, Stratiomyidae, and Syrphidae may be heavily represented in numbers of individuals, and the list of dipterous families does not end there. The abundance of individuals of numerous species of Diptera is because they are low in the food web. Those dipterous larvae that feed as predators are much less abundant. Adults and larvae of aquatic Coleoptera (Hydrophilidae, Dytiscidae, Scirtidae) are known from some bromeliad phytotelmata, as are adults and nymphs of Veliidae (Hemiptera). Fewer aquatic coleopterous families and far fewer species are reported from treeholes and Heliconia bracts. Nymphs of Trichoptera are recorded from bromeliad phytotelmata, and nymphs of Odonata from bromeliads and treeholes.

Phytotelmata inhabitants exhibit a full range of specialization. Some species inhabit many kinds of water bodies, whereas others inhabit only small bodies of water. Among the latter, some inhabit various kinds of phytotelmata, whereas the ultimate specialists inhabit only one kind (for example, only bracts of one or more species of Heliconia). The means by which most specialist insects select the places in which to oviposit is unknown. However, perception of volatile chemicals plays a role in some, and vision, including color vision, in some. Flightless invertebrate animals may have little control in the matter of dispersing from one phytotelm to another, beyond hitching a ride (phoresy) on some larger, more mobile organism that just may be about to disperse to another phytotelm.

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Phytotoxemia

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Symptoms of plant disease that are induced from the effects of insect/mite feeding and introduced salivary compounds (phytotoxins) are called phytotoxemias or plant toxemias. Categories of phytotoxemias include: (i) local lesions at the feeding point; (ii) local lesions with development of secondary symptoms; (iii) tissue malformations; and (iv) translocated phytotoxins. An arthropod that is capable of producing a phytotoxemia is sometimes described as being "toxiniferous."

Phytotoxemias are almost entirely produced by arthropods that suck plant fluids, and primarily involve Hemiptera. Some Hemiptera, gall making insects found within other orders, and some mites (Tetranychidae and Eriophyiidae) are also considered capable of producing certain phytotoxemias.

The nature of the toxins involved in a phytotoxemia is little understood, but apparently often includes enzymes adapted to the insect diet that have adverse effects on the host. Various pectinases, proteases, amylases, saccarhases, lipases and pheonolases are among the compounds identified that produce phytotoxemias. The effects of such phytotoxic compounds may vary depending on the response of the host plant. For example, the potato/tomato psyllid, *Paratrioza cockerelli*, is a species that produces serious systemic injuries to potatoes and tomatoes, but has little effect when feeding on eggplant and pepper.

Induction of a phtytoxemia is usually related directly to the presence of the insect responsible, and once the insect is removed no further damage occurs. However, if the damage is severe the plant may not recover. To prevent a phytotoxemia, usually the insect must be prevented from feeding, or killed soon after it begins feeding. In some cases, plant varieties are known that are resistant to injury.

Phytotoxicity

Damage to a plant due to contact with a chemical toxin.

Piceous

Very dark, black.

Pickett, Allison Deforest

A.D. Pickett was a pioneer in the field of insect pest management, but his important contributions to minimizing pesticidal inputs into crop production have often been overlooked. Pickett was born in Lower Kars, New Brunswick, Canada, in 1900. He attended Nova Scotia Agricultural College, Ontario Agricultural College, Macdonald College, and was granted a B.Sc. from McGill University in 1929. He worked at the Dominion Entomological Laboratory and was appointed the first Provincial Agricultural Representative for Kings County, Nova Scotia. He served as the Provincial Entomologist for Nova Scotia from 1929 to 1939, and developed into an outstanding teacher of zoology and genetics at the Nova Scotia Agricultural College. During this period he also served as extension entomologist. From 1933 to 1937 he served as Head of the Horticulture and Biology section and conducted graduate research on apple maggot strains, for which he was awarded a M.Sc. degree from McGill University in 1936.

Pickett was appointed Officer-In-Charge of the Dominion Entomological laboratory in 1939 and then Head in 1950. During this period he led a very productive research team at Kentville focusing on integration of biological and chemical control of fruit pests. For this innovative research in an era when chemical insecticides were highly regarded, Pickett was awarded an honorary D.Sc. degree from McGill University in 1959. The program that became known as "Pickett's modified spray program" earned him international recognition.

Pickett was honored by the naming of the A.D. Pickett Entomological Museum and Research Laboratory at Nova Scotia Agricultural College in 1984. He reciprocated by endowing the W.H. Brittain Memorial Fund at Macdonald College in recognition of the support and inspiration from Professor W.H. Brittain of Macdonald. Lastly, Dalhousie University of Halifax, Nova Scotia, awarded him an honorary L.L.D. degree in 1989. He died on September 18, 1991.

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Pickleworm, *Diaphania nitidalis* (Stoll) (Lepidoptera: Pyralidae)

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Pickleworm is a tropical insect which occurs widely in Central and South America and the Caribbean. It can survive in subtropical climates, such as the southernmost USA, but regularly survives the winter in the USA only in southern Florida and perhaps south Texas. Pickleworm is highly dispersive, and invades much of the southeastern USA each summer. Although it regularly takes 1 or 2 months for the dispersing pickleworms to move north from Florida to the Carolinas, in some years they reach locations as far north as Michigan and Connecticut. Presumably they are assisted in their northward dispersal by favorable wind patterns. In Canada, pickleworm has occasionally been found in southern Ontario. In Puerto Rico, it is more common in the mountains than at low elevations, and is not found at all in dry areas of the island.

Life History

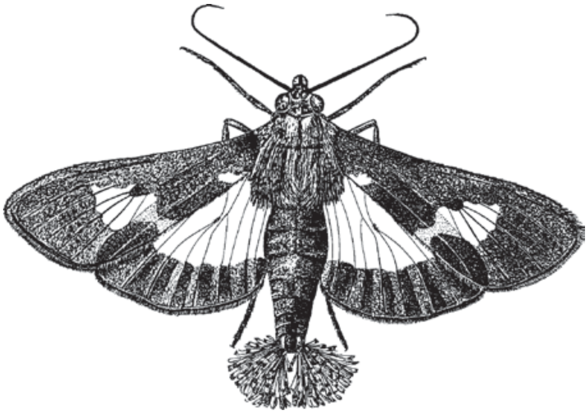
The pickleworm can complete its life cycle in about 30 days. Over much of its range, multiple and overlapping generations may occur annually, but as few as one generation occurs at the limits of its range.

The eggs are minute, measuring only about 0.4–0.6 mm wide and 0.8 mm long. The shape varies from spherical to flattened. Their color is white initially, but changes to yellow after about 24 h. The eggs are distributed in small clusters, usually 2–7 per cluster. They are deposited principally on the buds, flowers, and other actively growing portions of the plant. Hatching occurs in about 4 days. Egg production is 300–400 eggs per female.

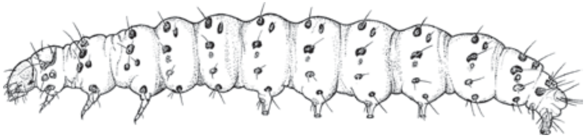
There are five instars. Total larval development time averages 14 days. Mean duration (range) of each instar is about 2.5 (2–3), 2 (1–3), 2 (1–3), 2.5 (2–3), and 5 (4–7) days, respectively. Head capsule widths for the five instars are about 0.25, 0.42, 0.75, 1.12, and 1.65 mm, respectively. Body lengths average 1.6, 2.5, 4.0, 10, and 15 mm during instars 1–5, respectively. Young larvae are nearly white in color with numerous dark gray or black spots (Fig. 56). The dark spots are lost at the molt to the fifth instar. Larval color during the last instar is somewhat variable, depending largely on the insect's food source. For example, they tend to be orange when feeding on blossoms, green when feeding on stem tissue, and white when feeding on fruit. Prior to pupation, larvae tend to turn a dark copper color. When mature, larvae often attain a length of 2.5 cm.

Pupation usually occurs in a leaf fold; often dead, dry material is used. There is only weak evidence of a cocoon, usually just a few strands of silk. The pupa is elongate, measuring about 13 mm in length and 4 mm in width. It is light brown to dark brown in color, and tapers to a point at both ends. Pupation usually lasts about 8–9 days.

Emerging moths fly during much of the evening hours, but most flight occurs 3–5 h after sundown, with peak flight at approximately midnight. The female moth produces a pheromone that attracts males, with peak production occurring at 5–7 h after sunset. Moths are fairly distinctive in appearance. The central portion of both the front and hind wings is a semi-transparent yellow color, with an iridescent purplish reflection. The wings are bordered in dark brown (Fig. 57). The wing expanse is about 3 cm. Both sexes often display brushy hairpencils at the tip of the abdomen. Moths are not found in the field during the daylight hours, and probably disperse to adjacent wooded or weedy areas during the heat of the day. Moths do not produce eggs until they are several days old.



Pickleworm, *Diaphania nitidalis* (Stoll) (Lepidoptera: Pyralidae), Figure 56 Adult pickleworm, *Diaphania nitidalis* (Stoll).



Pickleworm, *Diaphania nitidalis* (Stoll) (Lepidoptera: Pyralidae), Figure 57 Young larva of pickleworm, *Diaphania nitidalis* (Stoll).

Pickleworm feeds only on cucurbits, but both wild and cultivated species are suitable hosts. Creeping cucumber, *Melothria pendula*, is considered to be an important wild host. Summer squash and the winter squash species are good hosts. Pumpkin is of variable quality as a host, probably because pumpkins have been bred from several *Cucurbita* species. The *Cucumis* species, cucumber, gherkin, and cantaloupe, are attacked but not preferred. Among all cucurbits, summer squash is most preferred, and most heavily damaged. Cultivars vary widely in susceptibility to attack, but truly resistant cultivars are unknown. Cucurbits are intolerant of cold weather. Although diapause is unknown in pickleworm, it is the lack of host plants during the winter months that functionally limits the distribution of pickleworm.

Pickleworm has several natural enemies, but none reliably suppress damage. Generalist predators such as *Calosoma* spp. and *Harpalus* (both Coleoptera: Carabidae), the soldier beetle *Chauliognathus pennsylvanicus* DeGeer (Coleoptera: Cantharidae), and the red imported fire ant *Solanopsis invicta* Buren (Hymenoptera: Formicidae) have been reported to be important mortality factors. Also, several parasitoids are known, including *Apanteles* sp., *Hypomicrogaster diaphaniae* (Muesebeck), *Pristomerus spinator* (Fabricius) (all Hymenoptera: Braconidae), *Casinaria infesta* (Cresson), *Temelucha* sp. (both Ichneumonidae), and undetermined trichogrammatids. The braconid *Cardiochiles diaphaniae* Marsh (Hymenoptera: Braconidae) has been imported from Colombia and released into Florida and Puerto Rico in an attempt to obtain higher levels of parasitism.

Damage

Pickleworm may damage summer and winter squash, cucumber, cantaloupe, and pumpkin.

Watermelon is an unusual host. The blossom is a favored feeding site, especially for young larvae. In plants with large blossoms, such as summer squash, larvae may complete their development without entering fruit. They may also move from blossom to blossom, feeding and destroying the plant's capacity to produce fruit. Very often, however, the larva burrows into the fruit. The larva's entrance is marked by a small hole, through which frass is extruded. The presence of the insect makes fruit unmarketable, and fungal or bacterial diseases often develop once entry has occurred. If larvae burrow into fruit just before harvest, their presence is difficult to detect, yet a considerable amount of larval growth and feeding damage may occur. When all blossoms and fruit have been destroyed, larvae will attack the vines, especially the apical meristem. Cantaloupe is not a preferred host, and larvae often seem reluctant to burrow into the fruit. Rather, they feed on the surface or "rind," causing scars. Thus, pickleworm is sometimes referred to as "rindworm."

Management

It is very difficult to scout for this insect and predict its appearance. Moths are not attracted to light traps, and pheromone traps have had limited success. Pheromone lures are not currently available commercially. The small eggs, night-flying behavior, and inability to trap the insect reliably lead most growers to depend on preventative applications of insecticides.

Cucurbit producers in areas where pickleworm damage is likely to occur usually apply chemical insecticides from the onset of fruiting through harvest. The internal feeding behavior of larvae, which is so difficult to detect at harvest, causes particular emphasis on prevention of damage. In areas that are on the fringe of the normal range there are many seasons when damage will not occur, but producers apply insecticides as a preventative measure because prediction of occurrence is so difficult.

Pollinators, particularly honeybees, are very important in cucurbit production, and insecticide application can interfere with pollination by killing honeybees. If insecticides are to be applied when blossoms are present, it is advisable to use insecticides with little residual activity, and to apply insecticides late in the day, when honeybee activity is minimal.

The entomopathogenic nematode *Steinernema carpocapsae* has been shown to effectively suppress pickleworm injury in squash. Nematode survival is quite good in large-blossomed squash, where the nematodes can kill the young pickleworm before it burrows into the fruit. This approach is probably ineffective for species with small, open blossoms such as cucumber, however, because the nematodes die quickly when exposed to sunlight. *Bacillus thuringiensis* will kill pickleworm, but is usually not recommended because the internal feeding behavior puts the feeding larvae beyond the reach of a stomach-active toxin.

It is possible to cover plants with screen or row covers to prevent moths from depositing eggs on the foliage. However, because the plants must be pollinated, usually by honey bees, some allowance must be made to leave the plants uncovered. Given the night-flying behavior of the moths and the daytime activities of honeybees, this is not a difficult task on a small planting but is prohibitive on large acreage.

Some growers are able to prevent plant injury through careful timing of their cropping cycle. By planting early, it is often possible to harvest part of the crop before pickleworms appear. Usually the crop is eventually infested, so some yield is lost. Plowing under of the crop residue is recommended to destroy pupae in the leaf debris.

Squash can be used as a trap crop to keep pickleworm from attacking cantaloupe, a less preferred host. Destruction of squash blossoms, or even the entire plant, should be done periodically to keep pickleworms from exhausting the food supply and then moving onto adjacent cantaloupes.

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Picture-Winged Flies

Members of the family Ulidiidae and Platystomatidae (order Diptera).

► Flies

Picture-Winged Leaf Moths (Lepidoptera: Thyrididae)

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Florida State Collection of Arthropods,
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Picture-winged leaf moths, family Thyrididae, total 794 species worldwide, nearly all tropical, with nearly half the species Indo-Australian (only a few species are in the Nearctic and Palearctic regions); actual fauna likely exceeds 1,200 species. There are six subfamilies: Simaethistinae, Whalleyaninae, Argyrotypinae, Thyridinae, Siculodinae, and Striglininae. The first three subfamilies are sometimes treated as separate families. The family is in the superfamily Pyraloidea in the section Tineina, subsection Tineina, of the division Ditrysia (sometimes placed in its own superfamily, Thyridoidea). Adults small to large (9–90 mm wingspan), with head scaling average; haustellum naked; labial palpi upcurved or slightly porrect; maxillary palpi 1- to 2-segmented. Maculation varied, often dark with light spots, or shades of brown to mimic dead leaves, or very colorful; many with wing margins irregular in shape, or leaf-like. Adults are diurnal or crepuscular. Larvae are leafrollers (one Australian species is gregarious), or borers in stems and flower racemes; a few are gall makers. A number of host plants are used. Only a few species are economic. The subfamily Whalleyaninae and its nominate genus *Whalleyana* are named after the British lepidopterist Paul E. S. Whalley.

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Pierce's Disease Of Grape

This bacteria disease of grapes is transmitted by certain leafhoppers.

► Transmission of Plant Diseases by Insects

Pieridae

A family of butterflies (order Lepidoptera). They commonly are known as yellows-white butterflies, yellows, whites, and sulfurs.

► Yellow-White Butterflies

► Butterflies and Moths

► Transmission of *Xylella fastidiosa* Bacteria by Xylem-feeding Insects

Piesmatidae

A family of bugs (order Hemiptera). They sometimes are called ash-gray leaf bugs.

► Bugs

Pile

Having a covering of thick, erect setae that give the appearance of fur (= setose or pilose).

Pileiform

Having the form of an umbrella-shaped cap (pileus) (= agariciform).

Pilifer

A small projection, resembling a small mandible, at each side of the clypeus in Lepidoptera.

Pill Beetles

Members of the family Byrrhidae (order Coleoptera).

► Beetles

Pillbugs and Sowbugs, or Woodlice (Isopoda)

The terrestrial isopods known as pillbugs and sowbugs in North America are collectively known as "woodlice" in Europe. The term "woodlice" conveniently depicts their relatedness and preferred habitat, and deserves wider recognition and use in North America. Consistent with this is the fact that many of the pillbugs and sowbugs now found in North America seem to be immigrants from Europe. Indeed, several species have become almost cosmopolitan.

Classification

Woodlice are arthropods in the subphylum Crustacea, whereas insects are in the subphylum Atelocerata. Like many other terrestrial arthropods, they are commonly confused with insects. However, they are more closely related to shrimp and crabs than to insects, as shown below:

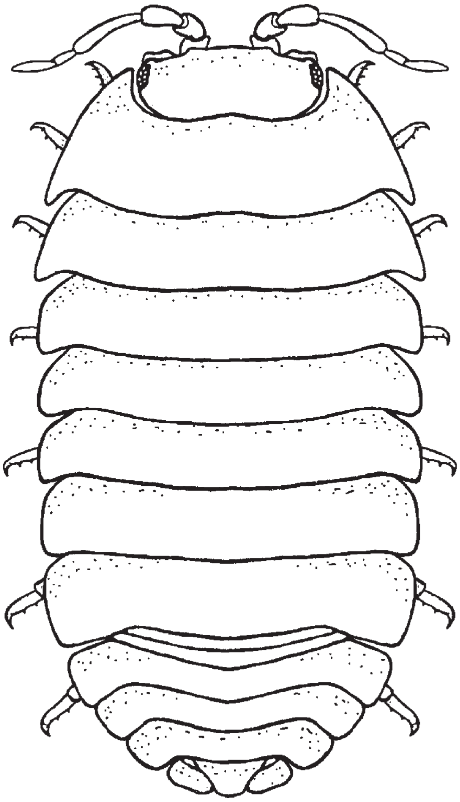
Phylum: Arthropoda
  Subphylum: Trilobita – Trilobites (these are extinct)
  Subphylum: Chelicerata
    Class: Merostomata – Horseshoe crabs
    Class: Arachnida – Arachnids (scorpions, spiders, ticks, mites, etc.)
    Class: Pycnogonida – Sea spiders
  Subphylum: Atelocerata
    Class: Diplopoda – Millipedes
    Class: Chilopoda – Centipedes
    Class: Pauropoda – Pauropods
    Class: Symphyla – Symphylans
    Class: Entognatha – Collembolans, proturans, diplurans
    Class: Insecta – Insects
  Subphylum: Crustacea – Crustaceans (isopods, shrimp, crabs, etc.)
    Class: Malacostraca
      Superorder: Peracarida – Amphipods, isopods, etc.
        Order: Isopoda

Class Malacostraca contains about two thirds of all crustacean species, including all of the larger forms. The three principal orders of malacostracans are the Isopoda, Amphipoda, and the Decapoda. The latter is best known to most people, as it contains the crayfish, lobsters, crabs and shrip. The woodlice are found in several families of Isopoda within the suborder Oniscidea. Many Isopods are marine, and a few live in freshwater habitats, but the member of the suborder Oniscidea are terrestrial. The members of the suborder Oniscidea are the most successful (diverse) of the land-dwelling Crustacea. The herbivorous and detritivores of the suborder Oniscidea are considered to be relatively primitive; the more advanced groups of Isopoda are carnivores, predators and parasites.

Life Cycle and Description

Though superficially similar to insects because they have a rigid exoskeleton and jointed appendages, there are some important differences. As in insects, the body of woodlice is divided into three major regions: the head, which bears the antennae and mouthparts; the thorax or pereion which bears the legs but never wings; and the abdomen or pleon. The head bears two pairs of antennae instead of the one pair found in insects, but one pair of the antennae in woodlice is greatly reduced in size and therefore not often observed. The pereion (thorax) consists of seven segments instead of the three found in insects, with each segment bearing a pair of legs ventrally. The pleon (abdomen) consists of six segments, but invariably is much smaller than the pereion. The ventral surface of the pleon bears plate-like structures, and is an important site for gas exchange. A terminal pair of tail-like appendages, called uropods, may be located at the tip of the pleon. Uropods are present in sowbugs but absent in pillbugs (Figs. 58 and 59). Sowbugs cannot completely roll into a ball, though pillbugs are capable of this behavior. Because they can roll into a ball, pillbugs are sometimes called roly-polys.

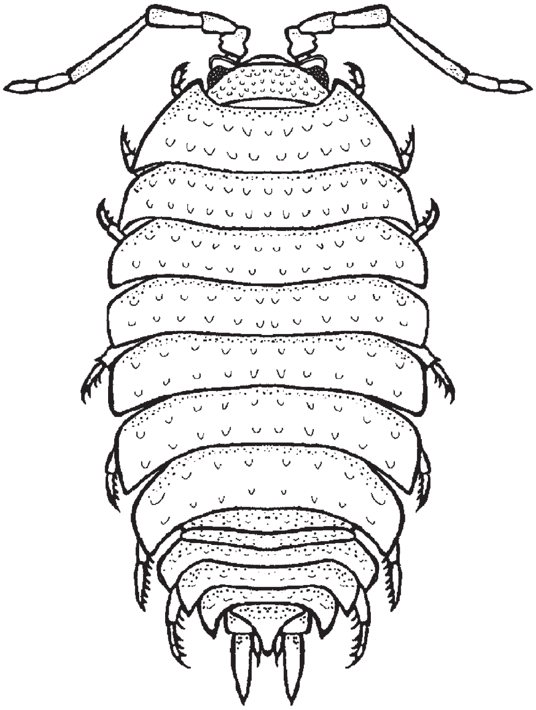
The female woodlouse carries her eggs and young about with her in a special compartment, called the marsupium, on the underside of her body. Fertilized eggs are inserted into the marsupium where the embryos (and later the young) obtain water, oxygen and nutrients from a nutritive fluid called, appropriately, marsupial fluid. The eggs may be up to 0.7 mm in diameter, and in some species over 100 eggs may be produced. The eggs persist for 3–4 weeks, then hatch, but the young remain in the marsupium for another 1–2 weeks before crawling out. They are only two mm in length at this stage of development. Woodlice commonly produce offspring 1–3 times/year, with spring and autumn broods most common. Woodlice often survive for longer than a year, with longevity of 2–5 years not uncommon.



Pillbugs and Sowbugs, or Woodlice (Isopoda), Figure 58 **An adult pillbug, *Armadillidium vulgare*.**

Woodlice often produce 20–40 young, and 1–3 broods per season. Brood size was positively correlated with female size. The young are highly gregarious, and sometimes cannibalistic. Once they have left the female they molt, usually within 24 h, acquiring a seventh pereion segment. After an additional 14 days a second molt occurs, and a seventh pair of legs is produced. Thereafter they do not change in morphology, other than to increase in size. The interval between molts is 1–2 weeks until the age of about 20 weeks, and molting continues irregularly for the remainder of their life, including adulthood. Molting occurs in two stages, with the posterior portion of the body shedding its old skin first, followed about three days later by the anterior portion.

Woodlice often attain a length of 8.5–18.0 mm as they reach adulthood. The width of the body is about half of its length. Woodlice are somewhat flattened and elongate oval in shape, seven pairs of



Pillbugs and Sowbugs, or Woodlice (Isopoda), Figure 59 **Adult of dooryard sowbug, *Porcellio scaber*.**

legs and 13 body segments are apparent, and they have long, jointed antennae. Eyes are evident on the side of the head. They are brownish or grayish in general body color, though often marked with areas of black, red, orange or yellow.

Ecology

Woodlice generally feed on dead plant material, though they also accept dead animal remains and dung, and occasionally ingest bacteria, fungi, and living plants. They are best viewed as decomposers, similar to earthworms, breaking down plant material and mixing it with mineral particles to produce soil. However, they are not the first organisms to attack leaf litter, waiting until microorganisms have begun the degradation process. Also, they sometimes have the unfortunate habit of grazing on plants, particularly seedlings. Woodlice occasionally attack seedlings above-ground, feeding especially on stems and young leaves, and below-ground, feeding on roots. Woodlice are most common in soils with neutral or alkaline pH, good crumb structure, high organic matter content, and where soil bacteria and other macrodecomposers such as earthworms and millipedes flourish. They tend to be absent from acid and waterlogged soil. Due either to the disturbance or lack of shelter, woodlice are virtually absent from thoroughly tilled land. On the other hand, straw or other coarse mulch provides good habitat for woodlice and can lead to crop damage. They have adapted well to humans and human habitations, and are often considered to be anthropophilic, but they also survive well in forests and grasslands, particularly if they can find shelter beneath logs and rocks. They are nocturanal.

Woodlice are parasitized by species of tachinids (Diptera: Tachinidae), with most displaying a fairly specific host range. Predation and cannibalism are known to occur, but it is uncertain whether these are important mortality factors in nature. Lizards, salamanders, shrews, spiders, centipedes, and ground beetles (Coleoptera: Carabidae) will eat woodlice. An iridovirus has been found to occur in woodlice populations in California. In addition to causing a slight blue to purple discoloration in infected woodlice, the longevity of infected hosts is greatly reduced when woodlice are infected with iridovirus. Fungus, nematode, and protozoan parasites seem to be of little importance.

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Pilose

Covered with soft hair.

Pine and Spruce Aphids

Members of the family Adelgidae (order Hemiptera).

- ► Aphids
- ► Bugs

Pine Tip Moths, *Rhyacionia* spp. (Lepidoptera: Tortricidae)

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There are approximately 35 known species of pine tip moths distributed throughout the palearctic and nearctic regions of the world. However, the greatest diversity of species within the genus *Rhyacionia* is found in the western United States. As their name implies, pine tip moths feed exclusively on pine trees. A few species are economically important, particularly in the southeastern and western United States.

Tip moth larvae feed within the buds and shoots of their host. Damage caused by tip moths is usually visible by the appearance of small accumulations of pine resin which collect around the entrance wound. The terminal portion of the infested shoot eventually turns brown as it is hollowed out by the burrowing larvae. The tree is normally not killed by this pest unless repeated, severe infestations occur. However, significant losses in growth and wood quality are common. Tip moths are primarily a problem in intensively managed pine plantations where slow growth and poorer wood quality can result in economic losses.

The biologies of tip moths within the genus *Rhyacionia* are similar. Adults normally emerge in spring from infested shoots, duff, or soil. The majority of species studied are univoltine, however, some have multiple generations per year. Adults are often inactive during much of the day, with mating generally occurring at dusk or later during the night. Females release a sex pheromone to attract males for mating. Oviposition occurs on the needles, buds, or shoots of the host tree. Eggs may be deposited singly or in clusters. First instar larvae generally mine the needles while later instars enter the shoot, feeding on pith and cambium tissue. Pupation occurs within the shoot, on or in the ground below the host tree, or in cocoons just below the soil, often attached to the root collar. Univoltine species generally overwinter as pupae on the ground. An important exception is the European pine shoot moth, *Rhyacionia buoliana*, which overwinters as a larvae in the buds, completing feeding the following spring. Multivoltine species usually spend the winter as pupae within the shoots.

The greatest diversity of species occurs in the southern Rocky Mountains in Colorado, New Mexico, and Arizona, most of which are associated with Ponderosa pine. However, the most economically significant tip moth species, the Nantucket pine tip moth, *Rhyacionia frustrana*, occurs in the eastern United States. This species attacks a number of pine species, but is primarily a problem on the vast acreage of intensively managed loblolly pine (*Pinus taeda*) plantations throughout the Southeast. For this reason, an extensive amount of research has been done on this pest compared to most other species of *Rhyacionia*, for which even the most basic information is lacking. Another significant pest is the European pine shoot moth, *Rhyacionia buoliana*, which was accidentally introduced into North America in the early 1900s. It is a sporadic pest of pine plantations in the Northeast, the Lake States, and the Pacific Northwest.

In most cases, prevention of pine tip moth infestations involves planting pines on suitable sites within their native range and avoiding intensive management practices (herbicides, pesticides, fertilizers, etc.). Chemical control is a viable option for preventing damage but has seldom been used historically due to a lack of perceived threat from these non-lethal forest pests. Recent research on Nantucket pine tip moth, however, has demonstrated that substantial growth losses can occur in pine plantations that receive repeated damage, even at seemingly low levels. These pests are likely to become more important in the future as forest management becomes increasingly intensive in order to meet the wood and paper demands of a rapidly growing population.

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Pine Weevil, *Hylobius abietis* Linnaeus (Coleoptera: Curculionidae)

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Hylobius abietis (Fig. 60) L. feed on the stem bark of conifer seedlings. In the absence of appropriate control measures, the damage may reach a level that rules out planting as a means of conifer regeneration. It is distributed throughout the coniferous forests of northern Eurasia, including the British Isles and Japan. Other *Hylobius* species cause damage of a similar type, both within this area, and in North America. Soon after the introduction of clear felling systems in Central Europe, damage by *H. abietis* became wide-spread.

Pine weevil adults are blackish brown, robust-looking insects with a body length between 9 and 14 mm. Their antennae are located near the tip of the snout. Small tufts of yellow hair form characteristic patterns on the thorax and the abdomen, but are often worn off in older individuals that have spent a long time burrowing in the soil. The yellowish-white larvae are footless, curved and wrinkled, with a brown head capsule. Fully grown, fifth instar larvae attain a body length of about 15 mm.

Pine Weevil, *Hylobius abietis* Linnaeus (Coleoptera: Curculionidae), Figure 60 ***Hylobius abietis*.**

Migration

Upon logging of coniferous trees, volatile substances such as terpenes emanate from stumps and logging debris, particularly in clear-cuts when temperatures rise at the onset of summer. These volatiles attract weevils that have emerged from their hibernation sites in the forest floor. A main migration flight, usually lasting for a week or two, starts when maximum temperatures approach 25°C. The weevils take off into the wind to drift along. They have been observed flying above the forest canopy and are likely to land when sensing the strong bouquet of conifer volatiles. Migrants may end up in the wrong place, such as lumberyards and newly built wooden houses, and at sawmills, they can be found in great abundance on heaps of fresh sawdust. However, a large part of the migrants reach areas with fresh conifer stumps, where a new generation of weevils can reproduce in the roots. After the spring migration the weevils rarely fly for the rest of the season.

Oviposition

As both sexes are attracted by volatiles from fresh stumps, they will meet in the immigration areas. It is doubtful that sex pheromones play a role, other than maybe at close range. Upon mating, an extensive period of oviposition starts using roots with a diameter of at least 1 cm. Clear-cut areas offer an abundance of suitable breeding substrate. During the growth season, a female may lay several dozen eggs, which are laid singly, either in small cavities that she gnaws in the root phloem, or simply in the soil. When the soil is dry, the latter option seems to be avoided. Egg larvae hatching in the soil apparently use chemical clues to find suitable roots and may cover considerable distances during their underground migration. Throughout the egg-laying period, the weevils feed on local vegetation, including conifer seedlings. In cool areas, the oviposition may come to a halt by the onset of winter, to be resumed the next spring in stumps that remain fresh enough. The adults may survive for two, or even three seasons.

Development

Inside the subterranean stump roots, the offspring is protected against extreme weather and some of their natural enemies. The weevil larvae go through five stages during which they dig long, winding galleries in the phloem and outer xylem of the roots. Ambient temperature determines the developmental speed: at a stable 23°C, they are full-grown 40 days after the egg is laid, while at 12°C, the development takes more than 100 days. In their last instar, which in warmer areas may be reached the first autumn, the larvae construct an oblong pupal chamber. In thick-barked roots, this is dug out at the interface between phloem and xylem; where root bark is thin, the chamber is excavated in the wood and the entrance is closed from the inside with a plug of frass. If temperatures stay below about 21°C during their fifth instar, the larvae enter a diapause, which is broken after hibernation. Thus, a diapause is a regular feature of the weevil life cycle in cold boreal forest soils. After pupation, the adults remain in the pupal chamber while their exoskeleton hardens. They may then make their way to the surface, but if hatching occurs late in the season, they over-winter in the pupal chamber. Pine weevils hibernate at various larval stages or as adults, but not as eggs or pupae. Before migrating to other areas with fresh breeding material, the young adults go through an intensive period of feeding to develop their energy reserves and sexual organs.

The prolonged period of oviposition, the temperature-dependant development, and the facultative diapause lead to a highly variable generation time. In southern Scandinavia and Finland, a 2-year life cycle dominates; in the north, generation time stretches to 4 years or more. A mountainous landscape adds to the variability because the microclimate of steep, sunny and shady slopes are quite different. The survival of the immature stages is related to the generation time; a prolonged development means a higher risk of parasitation and predation, as well as increased competition from root-inhabiting fungi and other insects. A prolonged presence of the parental generation and a highly variable development of their offspring mean that the population remains high for several years. This is reflected in the period of damage.

Damage to the Conifer Seedlings

The adult pine weevil damages seedlings by eating the phloem of the above-ground stem. Moderate stem feeding often results in small, irregular "pockmarks" in the bark. A healthy plant may survive this damage and callus tissue soon covers the wounds. Severe attacks can girdle the stem, thereby interrupting photosynthate translocation and impairing water flow in the seedlings. The weevils prefer larger seedlings over smaller, but the former generally survive better. The damage occurs in natural regeneration as well as on planted seedlings, but in the former case, it often goes unnoticed because of an abundance of seedlings. Attack on planted seedlings is more likely to be noticed and generally has more serious consequences because the plants are distributed at an economically set distance. Both endemic and introduced coniferous species are attacked, as well as a number of other trees and weeds. Popular names in Europe often refer to the conifer that is most commonly attacked. As opposed to the stem feeding, larval tunneling in the roots can be considered useful because it accelerates stump decomposition and nutrient recycling.

If planted seedlings are not given appropriate protection, the mortality rate may be unacceptably high (for example, in southern Scandinavia, the mortality frequently exceeds 50%). The damage is often patchy, resulting in gaps in the future forest stand. The severity of damage is influenced by a variety of factors: the local environment and silvicultural practices both play a role. Regionally speaking, the damage is more severe in the southern parts of the pine weevil's range, probably due to more favorable conditions for the immature stages. Ground vegetation may be important, since the weevils can feed on a variety of plants. Upon clear cutting on lush sites, when thick vegetation is cut back, the ground vegetation will often succumb to sun-exposure, leaving new-planted seedlings as an extra welcome food for the weevils. Burned areas are particularly prone to damage. The common practice of extending felling coups from year to year facilitates migration to nearby breeding sites and in such cases, the population may build up to very high levels. Damage may become so severe that planting must be postponed for years. This practice, known in German as "Schlagruhe," may imply serious weed problems on sites with thick vegetation.

Control

Before World War II, a wide variety of control methods were used, including removing stumps, digging trap pits from which the weevils could not escape, using fresh stem sections and bark pieces to lure the insects, and a wide variety of stem treatments, including mechanical as well as chemical. After World War II, stem application of DDT was thought to solve the pine weevil problem for the future. DDT was thought to be both efficient and harmless. At least in more northern regions, the protective effect of DDT lasted for 2 years, protecting the seedlings during the most critical periods. Lindane (γ-BHC) was added to the compounds to accelerate the killing. When these chlorinated hydrocarbons were banned for environmental reasons in the 1970s, pyrethroids such as permethrin became the preferred chemicals. Although pyrethroids do not accumulate in food webs like the chlorinated hydrocarbons, environmental groups oppose their use, even when they are applied in nurseries. The European Commission may not allow the use of permethrin for forest seedling protection in the future.

Currently, the alternatives to insecticides are a mixed bag of silvicultural and technical methods. Substitution of clear felling and planting with natural regeneration methods would reduce the problem. However, this is often difficult in spruce forests because the shallow-rooted seed trees that are left are prone to wind felling. More deep-rooted species, e.g., Scots pine, are indeed often naturally regenerated. Here, a moderately dense shelterwood stand may significantly reduce seedling damage. This is partly due to the weevils' feeding on twig bark in the canopy and on superficial tree roots. Soil scarification also reduces feeding, particularly where seedlings are planted in exposed mineral soil. This effect diminishes gradually as the scarified patches fill up with vegetation and litter. Planting on small mounds of mineral soil is an improvement of the scarification method, though expensive. A variety of stem protecting devices exist, including coats of wax or latex, and various objects made from plastic, paper, etc., that are fitted around the seedling. At present, none of these devices seem to be reliable for a prolonged period of time; some are efficient for one season, but fail the next. Some of the designs may cause damage to the plant roots.

The pine weevil has a variety of natural enemies, such as parasitoids, and invertebrate and vertebrate predators. However, these organisms rarely seem to make significant inroads on the populations. In some cases, this may be because the immature stages are relatively inaccessible in their subterranean hiding places. Fungi and nematodes kill weevils, and nematodes may possibly become an active means to destroy the soil-dwelling stages, provided strains can be found that are active in cool soils. The artificial application of fungi to occupy the phloem of stumps could render this substrate less useful for the larvae, but success depends on how fast the hyphae are able to permeate the substrate. Considerable efforts are allocated to the search for chemicals with repellant and antifeedant properties, potentially to include them in stem protectants. Recently, a repellent substance has been patented, which occurs in excrements that the egg-laying females deposit next to their eggs, probably as a warning to other pine weevils. It seems unlikely that the pine weevil will easily adapt to this natural signal.

A panacea to the pine weevil problem does not seem likely. In areas where clear cutting remains a dominant way of regenerating conifers, the pine weevil is likely to retain its unique position as a headache for foresters and an expensive enemy of commercial forestry.

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Pine Wilt

This is an insect-transmitted disease of pine trees caused by nematodes.

► Transmission of Plant Diseases by Insects

Pine-Flower Snout Beetles

Members of the family Nemonychidae (order Coleoptera).

► Beetles

Pin-Hole Borers

Some members of the subfamily Platypodinae (order Coleoptera, family Curculionidae).

► Beetles

Pink Hibiscus Mealybug, *Maconellicoccus hirsutus* Green (Hemiptera: Pseudococcidae)

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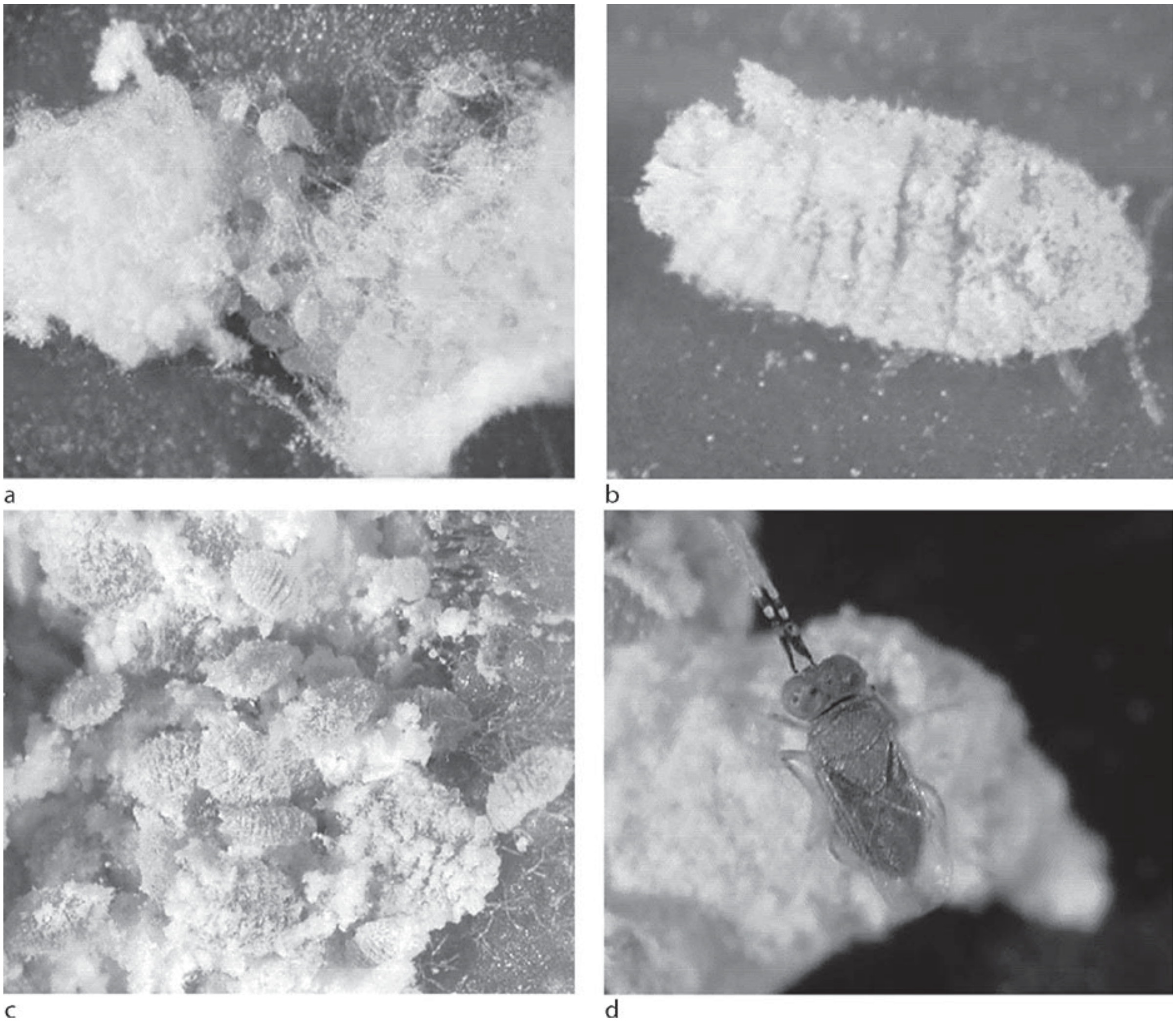
The pink hibiscus mealybug, *Maconellicoccus hirsutus* (Green), is native within the area encompassing Southeast Asia and nearby Australia. Its host range is very large, exceeding over 200 perennial and annual plant species, many of which are important in agriculture and as ornamentals. During the early part of the twentieth century, its range extended into Central Asia and Egypt. Within Egypt, it was a very significant pest of several common plant species, including cotton. Initially, a predatory beetle species (*Cryptolaemus montrouzieri*) was reared and introduced in large numbers. This provided some short-term relief; however, it was not until several parasite species were introduced that high levels of control were sustained. The pink hibiscus mealybug appeared first in the Western Hemisphere in Hawaii in 1984 and in the Caribbean island of Grenada and neighboring islands in 1994. In subsequent years, it spread to over 27 island countries in the Caribbean and in 1999, it was found in southern California, USA, the adjoining border region of northern Mexico, and the Central American country of Belize. By 2000, it was discovered in the Bahamas and northern South America (i.e., Venezuela/Guyana region), and attained Florida, USA, in 2002.

Female pink hibiscus mealybugs pass through three immature nymphal stages prior to developing into wingless adults. Most commonly, egg masses (i.e., ovisacs) (Fig. 61) containing several hundred eggs are laid at nearly the same location on a plant where the female developed. They lay one ovisac during their life. Total egg production ranges widely and is dependent on the host plant. Several hundred eggs are produced by females that have developed on potato sprouts, whereas 600 or more eggs often are laid by females that have developed on pumpkin fruit. At temperatures ranging from 26 to 33°C, the total development time from egg to gravid female takes 4–5 weeks. This includes approximately 5 days for egg hatch, 7 days for first and second instar female nymphs, 8 days for third instars and approximately another week for adult females to fully mature and begin laying eggs. As adults, females undergo a considerable increase in size (approximately 2- to 3-fold) prior to laying eggs. In contrast, although male pink hibiscus mealybugs look essentially identical to female mealybugs as first instars and most of the second life stage, male nymphs take on a considerably different appearance as late second instar nymphs. They become elongate and begin to sport small wing buds that become accentuated in third and fourth instars. As late second instars to the time males emerge as winged adults, they live clustered together as small groups within flocculent mounds of waxy material. During these late stages of development, the males are developing within a cocoon-like structure. Females also produce an abundant white, waxy substance that covers their bodies. Male pink hibiscus mealybugs have four immature nymphal stages. There is a third instar life stage of very short duration (lasting for little more than a day) and a fourth nymphal life stage lasting for 5–6 days prior to emerging as a winged adult.

First instar nymphs are referred to as crawlers because they are very actively moving at this stage. The crawlers and all other immature stages range in color from orange to medium pink. Adult females have a very dark pink coloration. Wax is present on all stages; however, it is especially abundant on third instar and adults. Although many mealybug species are field identified by specific patterns of wax filaments extending from the perimeter of the body or very long filaments extending from the posterior, the pink hibiscus mealybug produces no distinct pattern of filaments. As a result of the delicate nature of wax filaments, field identification of mealybug species typically requires viewing the characteristics of numerous individuals in a group as opposed to one isolated mealybug. The life stage of preserved pink hibiscus mealybug specimens can be accurately identified by the number of antennal segments. First and second instar nymphs have six segments, third instar females have seven segments, whereas adult females have nine-segmented antennae.

The pink hibiscus mealybug undergoes numerous generations each year. Population increase is dependent on temperature and



Pink Hibiscus Mealybug, *Maconellicoccus hirsutus* Green (Hemiptera: Pseudococcidae), Figure 61 Pink hibiscus mealybug (*upper left*) ovisac, (*upper right*) young adult female, (*lower left*) cluster of nymphs and adult females, (*lower right*) parasitoid *Anagyrus kamali* female.

suitability of host plants, which is often linked to moisture availability. The pink hibiscus mealybug performs well at moderate to high temperatures (exceeding 38°C). In the tropical and subtropical regions, this mealybug species reproduces continuously throughout the year, having abundant host plant material and temperatures ranging from 22°C and above. In the more temperate areas of its distribution in the northern hemisphere, the pink hibiscus mealybug population is difficult to find from winter to late spring. From June to September, population densities may increase dramatically in the absence of effective natural enemies. From November onward, the population declines as certain host species (especially mulberry) drop their leaves, causing the mealybugs to move from the growing regions of the tree (i.e., branch terminals) to larger branches that often contain crevices in rough bark, well suited for providing protection. Essentially all life stages are present during the winter period, although later instars and adult female mealybugs are more common.

As previously stated, *Cryptolaemus montrouzieri* is cited as an important biological control agent within its presumed native range. It has also been used with some success within new regions where the pink hibiscus mealybug has become established. Parasites also play a very important role in population regulation. *Anagyrus kamali* (family Encyrtidae) is among several agents that have had a long-term impact on the pink hibiscus mealybug in Egypt and has been the most important natural enemy introduced to date to control the pink hibiscus mealybug in the Western Hemisphere. This parasitoid has reduced mealybug population densities by 90% or more in St. Kitts, West Indies; St. Thomas and St. Croix in the U.S. Virgin Islands, Puerto Rico, Belize, Bahamas and California, USA, resulting in a highly successful biological control program.

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Piophilidae

A family of flies (order Diptera). They commonly are known as skipper flies.

► Flies

Pipunculidae

A family of flies (order Diptera). They commonly are known as big-headed flies.

► Flies

Piroplasmosis: *Babesia* and *Theileria*

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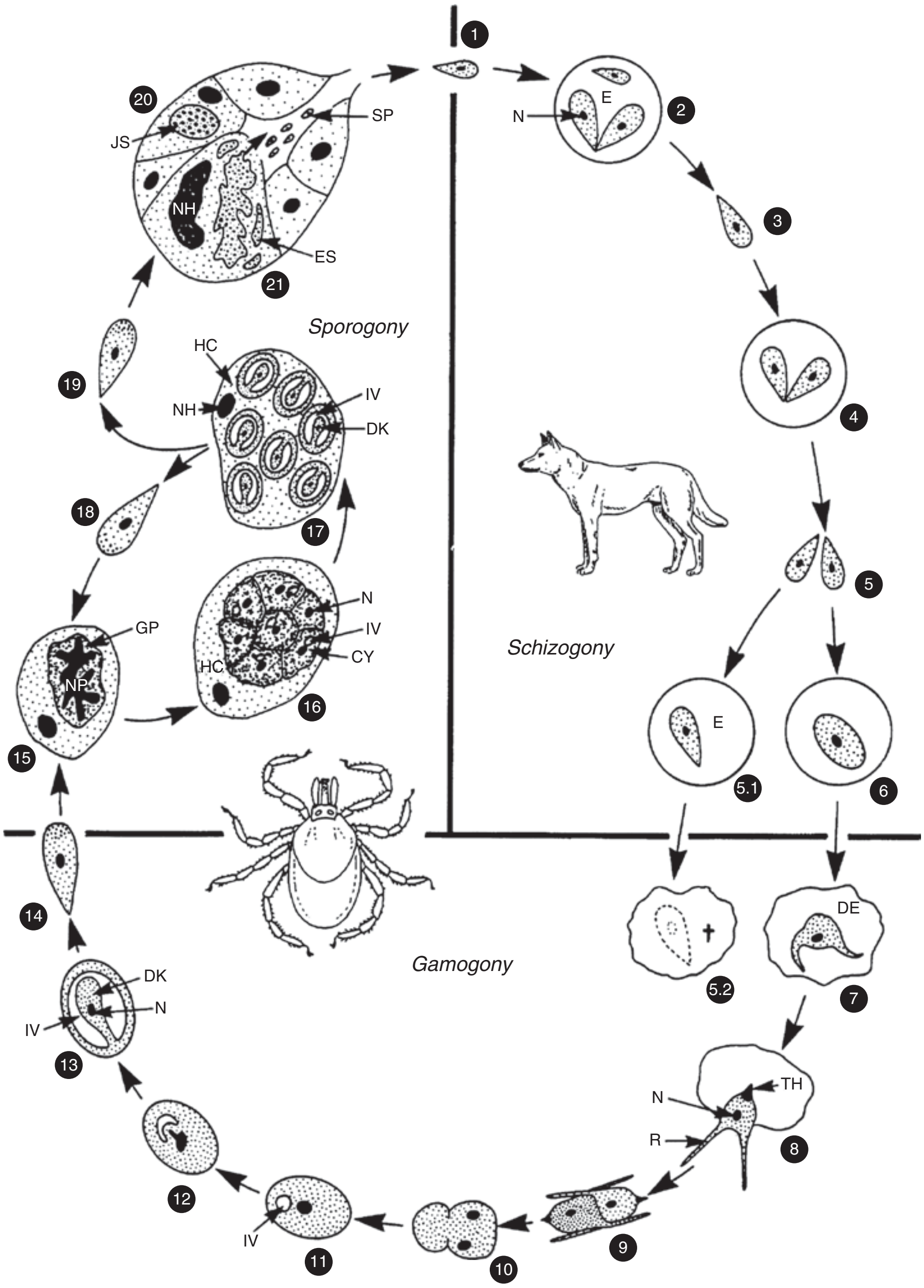
The Piroplasmea, a class of protozoa, are transmitted to vertebrates by ticks. Piroplasms infect erythrocytes (RBCs), and some also attack leukocytes. Species from two genera, *Babesia* and *Theileria*, cause serious diseases in dogs, cattle, sheep, and goats.

Babesia

Some 99 species of *Babesia* are parasites of nine orders of mammals. We shall consider only those species that cause babesiosis in dogs, ruminants and humans.

Canine babesiosis, also known as canine piroplasmosis or malignant jaundice, is caused by *Babesia canis* and *B. gibsoni*. The former is cosmopolitan, especially in warm climates, while the latter is found in Asia and North America. Both are pathogenic in dogs. *B. canis* is transmitted by the brown dog tick *Rhipicephalus sanguineus*. The extent of pathology in the dog is dependent on the virulence of the strain of *B. canis*.

The life cycle of *Babesia canis* is typical of other species of *Babesia*. The sporozoite is introduced into the vertebrate host via the saliva of *R. sanguineus*. Sporozoites invade the host's RBCs where they develop via binary fission into merozoites. Eventually these RBCs rupture, releasing the parasites to invade other RBCs. Merozoites develop into gamonts in some RBCs. Gamonts infect ticks when a bloodmeal is taken. The



Piroplasmosis: *Babesia and Theileria*, Figure 62 **Diagram of the life cycle of Babesia canis. An infectious tick introduces sporozoites (1) into the blood of its host and the sporozoites; they undergo binary fission in the red blood cells (RBCs) (2–4); the merozoites differentiate into gamonts also within RBCs (5, 6). When infectious blood is ingested by a tick, gamogony and fertilization occur in the gut of the tick (7–13), and then the kinete (14) enters cells of the salivary gland where sporogony takes place (15–20). Abbreviations: CY, cytomere; DE, digested RBC; DK, developing kinete; E, RBC; ES, enlarged sporont forming sporozoites; GP, growing parasite or polymorphic stage; HC, host cell; IV, inner vacuole; N, nucleus; NH, nucleus of host cell; R, raylike protrusion; SP, sporozoite; Th, thornlike apical structure; YS, young meront. (From Marquardt et al. (2000), used with permission of Harcourt Academic Press.)**

development of sporozoites into gamonts is an asexual form of reproduction known as schizogony. It allows the rapid build-up of the parasite in the host. Within the tick's midgut, sexual reproduction occurs in a process known as gamogony. The fertilized kinete then enters cells of the salivary gland where sporogony takes place. This is a process of asexual reproduction that results in the production of large numbers of sporozoites. The kinete can also infect the ovaries which allows transovarial transmission to new larvae and produces a new generation of infected ticks. Babesia canis are also transmitted from one life stage to another in a process named transstadial transmission.

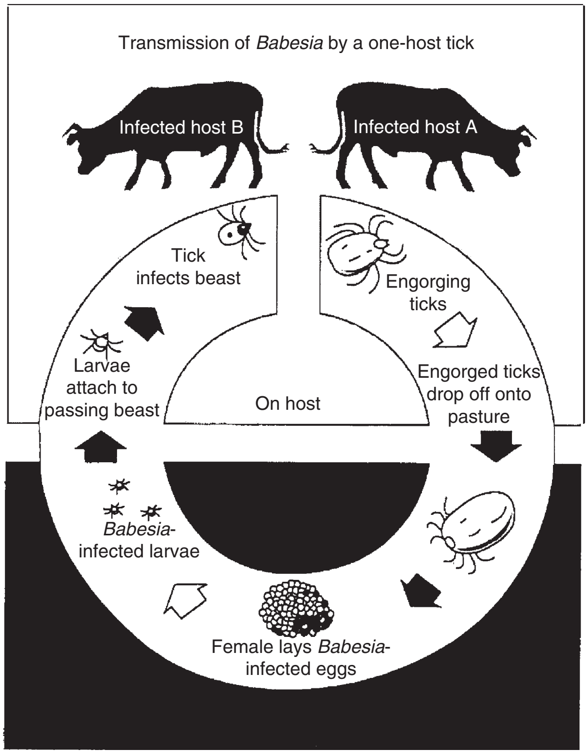
Most of the symptoms of the different babesioses including canine babesioses, can be traced to the breakdown of infected RBCs and the release of toxic products. This can result in anemia, enlarged spleen, kidney damage and sometimes impaired circulation of blood. Dogs that recover from canine babesiosis are immune to future infections. As with other babesiosis, diagnosis is made by identifying the parasite within RBCs. Several drugs are effective against canine babesiosis.

Two species of *Babesia* are parasites of sheep: *Babesia motasi* and *Babesia ovis*. Some strains of *B. motasi* will infect goats as well as sheep. *Babesia motasi* produces a severe disease but is even more pathogenic when it is accompanied by infections of *Theileria* and or *Ehrlichia*. *Babesia ovis* is found in equatorial Africa north to the Sahara, in the Mediterranean area throughout Europe, and portions of the former USSR. It is believed to be transmitted by *Rhipicephalus bursa* and *R. evertsi* outside of Asia, and *R. bursa* in the former USSR. The latter tick can transmit *B. ovis* transovarially through at least 44 generations. *Babesia motasi* occurs in equatorial Africa north to the Sahara, the Mediterranean area and Europe. It is believed to be transmitted by species of *Haemaphysalis* in Europe. Sheep infected with *Babesia* can act as carriers for up to 2 years.

Horses and other equids are infected by *Babesia caballi* which causes equine piroplasmosis worldwide. Mortality in domestic horses is less than 50%, but strains with differing virulence exist. Over ten species of ticks can vector *B. caballi*. *Dermacentor nitens* transmits the parasite in the United States, Central and South America.

Bovine babesioses is caused by seven species of *Babesia* and is transmitted by several species of ticks. Domestic cattle are at high risk from babesiosis worldwide. Two of the seven species that cause bovine babesiosis, *Babesia bovis* and *Babesia bigemina*, are widely distributed in Africa, Asia, Europe, Australia and Central and South America. *Babesia bovis* is transmitted by species of *Boophilus*, especially *B. microplus* and *B. decoloratus* in tropical and subtropical areas, and by *Rhipicephalus bursa* in southern Europe. Transmission by a one-host tick such as *B. microplus* and other species of *Boophilus* is described in the accompanying figure. The female tick becomes infected during feeding and transmits the pathogen transovarially to larvae that infect cattle as they feed. Many factors are related to the success of this transmission cycle (Fig. 63).

Babesia bigemina causes Texas cattle fever, also known as Red water fever or splenetic fever. Feeding ticks transmit the parasite. The African strain of *B. bigemina* is the most pathogenic, the Australian strain less so. The tick vector in the USA is *Boophilus annulatus*. Texas cattle fever is important historically because it is the first disease caused by a protozoan parasite that was shown to be transmitted by a blood feeding arthropod. The disease was first noticed during the cattle drives in the mid 1800s, and was officially described in 1888 as Texas cattle fever. Efforts to eradicate Texas cattle fever started at the turn of the century with the goal of eliminating the disease in the southeast part of the country, especially Texas and Florida. The ability to control cattle movement into Florida resulted in success in eliminating Texas cattle fever in that state by the 1930s. Because of its long border with Mexico, control of cattle movement into Texas was more difficult. Even so, the disease has largely been eliminated as a problem though there is still a sub-symptomatic level of infection in some Texas herds.



Piroplasmosis: *Babesia* and *Theileria*, Figure 63 **Diagrammatic representation of the transmission of a *Babesia* species by a one-host tick. The upper half shows the ticks attaching, feeding, and dropping from the host, while the lower half shows the events that occur in the pasture. Factors affecting the success of the transmission cycle include: (1) the concentration of infected erythrocytes; (2) number of infected, replete females dropping from the diseased host; (3) proportion of engorged females that lay eggs; (4) proportion of eggs that hatch; (5) the proportion of the larval population that is infected with the pathogen; (6) the number of infected larvae attaching to susceptible bovine hosts each day; (7) host immunity (natural and acquired) to infection; and (8) host resistance to tick parasitism. (From Sonenshine (1993), used with permission of Oxford University Press.)**

Five other species of *Babesia* are not distributed as widely as *B. bovis* and *B. bigemina*. *Babesia major* occurs in Europe and the Middle East where it causes a disease in cattle with limited mortality. *Haemaphysalis punctata* vectors *B. major* which is transmitted transovarially in the tick. *Babesia jakimovi* occurs in Siberia where it causes a disease in cattle that has high mortality. It is transmitted by species of *Ixodes*. The pathogen is transmitted transovarially in its vectors. Adults of the next generation of ticks are the infective stage. *Babesia divergens* occurs in Europe and causes a disease that can produce a parasitemia in cattle with as high as 24% of RBCs infected. The pathogen is transmitted by *Ixodes ricinus*. The adult tick picks up the pathogen during feeding and transmits it transovarially. All feeding stages of the next generation can transmit the pathogen to cattle. *Babesia ocultans* occurs in South Africa, and *Babesia ovata* in Japan.

Clinical symptoms of babesiosis are seen 8–16 days following infection. Most of the symptoms result from infected RBCs which eventually break down releasing hemoglobin and metabolic byproducts of the parasite. This results in a fever that can rise to over 40°C and anemia. Hemoglobin creates the characteristic red tinge of the urine. *Babesia bovis* infections can produce a hypertensive shock syndrome where sick animals quit feeding and become listless. Often dry bloodstained feces occur. Parasitized animals may develop sunken eyes and muscle tremors. Symptoms can be severe especially in older animals. Newborn calves are protected by maternal antibodies.

Cattle are able to develop immunity to infection with *Babesia* species. Persistent subclinical infections causes acquired immunity. Calves also get immunity from their mothers that can last several months, and if infected, calves develop an even stronger immunity that can last for up to 4 years. Some breeds of cattle are naturally more resistant to the disease, so they are preferred in areas where there is a high level of infected ticks. Currently the best control of the disease is by dipping and spraying the animals to control tick infestations. A vaccine used in Australia has had some success.

Four species of *Babesia* have been found in humans: *B. bovis* and *B. divergens* whose normal host are oxen, *B. equi* whose normal host are horses, and *B. microti* whose normal host are rodents. Piroplasmosis in humans is rare and those without a spleen are the most susceptible. *Babesia microti* can infect individuals with a normal spleen. *Babesia microti* is transmitted by *Ixodes ricinus* and *I. trianguliceps* in Europe, and *I. scapularis* in the USA. Symptoms of human babesiosis are similar to those of malaria, but the disease lacks the periodicity found in malaria.

Theileria

Theileria spp. are parasites of domestic and wild ruminants, and domestic and wild felines. Six species infect cattle: *Theileria parva*, *Theileria annulata*, *Theileria orientalis*, *Theileria mutans*, *Theileria taurotragi* and *Theileria velifera*. The most serious diseases are caused by *T. parva* and *T. annulata*. These two pathogens are considered later. *Theileria orientalis* occurs worldwide and is transmitted by several ixodids. In western Eurasia, through the northwest of Africa, it is transmitted by *Haemaphsalis punctata*, but in the eastern Asia and Australia it is transmitted by *H. longicornis*. Usually *T. orientalis* causes a mild disease, but in susceptible breeds of cattle it can produce a severe anemia. *Theileria orientalis* may be a synonym of *T. buffeli* and *T. sergenti*. *Theileria mutans* occurs throughout tropical Africa. Its principle vector is *Amblyomma variegatum*. *Theileria mutans* is usually not very pathogenic, although a pathogenic strain of the parasite exists in East Africa that can produce severe anemia with up to 45% of the host's RBCs infected. *Theileria taurotragi* infects cattle in eastern, central and southern Africa, and can also infect sheep and goats. The pathogen is transmitted by *Rhipicephalus appendiculatus*, *R. zambeziensis* and *R. pulchellus*. *Theileria taurotragi* produces a mild or subclinical disease in cattle but can produce a fatal disease in eland. *Theileria velifera* is found throughout Africa south of the Sahara. It is transmitted by *Amblyomma variegatum*, *A. hebraeum* and *A. lepidum*. The parasite causes a disease of low pathogenicity. *Theileria cervi* is a parasite of cervids in Europe and the United States. In the USA the pathogen is transmitted by *Amblyomma americanum*. The pathogen is common in white-tailed deer (*Odocoileus virginianus*) in the south and southeastern states. No clinical manifestations of these infections occur.

Theileria parva causes East Coast Fever, the most serious of the diseases caused by *Theileria* in cattle. It is transmitted by *Rhipicephalus appendiculatus*. East Coast Fever was first described in east Africa at the start of the seventeenth century. By 1901–1902 it had spread to southern Africa. The incubation period for East Coast Fever is 10–25 days. Symptoms include fever, swollen lymph nodes and emaciation. Most of the damage is to the lymphatic system, especially the lymph nodes and spleen, but other organs including the kidney, lungs and liver may also be affected. Older animals are more susceptible to East Coast Fever than younger animals. The most common control of East Coast Fever is to kill the vector ticks. Antigenic diversity exists in *T. parva*, and this can complicate the outcome of the disease. In addition, strains of *T. parva* exist that have different virulence. Virulence is also tied to the tick vector, and some ticks only transmit a 100% fatal form of the parasite. The disease is believed to have originated in African buffalo *Syrlcerus caffer* which acts as a reservoir. East Coast Fever is a benign disease in the buffalo.

An important concept in understanding East Coast Fever is endemic stability, which is defined as the condition in a given cattle herd (or population) where a large majority of individuals become infected and immune by 6 months of age, with little or no clinical symptoms. Endemic stability occurs when the cattle have a low innate susceptibility to the pathology of East Coast Fever; when *R. appendiculatus* infestation occurs throughout the year; and when most of young calves are exposed to a low *T. parva* challenge. Eradication of the tick vectors in endemic areas can result in the loss of endemic stability. Subsequent relaxation of control measures in these areas has often resulted in a rapid increase in the tick population with the return of severe epidemics of East Coast Fever.

The life cycle of *Theileria parva* is similar to that of *Babesia canis*, but differs in that lymphocytes are invaded as well as RBCs. The infectious stage of the parasite is the sporozoite. These first invade lymphocytes in the lymph nodes, unlike *Babesia canis* sporozoites. In lymphocytes, the sporozoites undergo schizogony and multiply, then invade RBCs. Erythrocytic schizogony is rare or absent. Infected RBCs are transmitted to the tick where they undergo gamogony and fertilization in the midgut, then invade salivary gland cells. Here sporogony occurs, resulting in sporozoites that are transmitted to the vertebrate host with the tick's saliva. In the tick vector, transstadial transmission occurs but not transovarial transmission.

Theileria annulata causes Mediterranean or tropical theileriosis in cattle. The pathogen is found throughout northern Africa, into the Middle East including Saudi Arabia, Turkey, southern Europe through the Caucasian area into India and China. It is transmitted by species of *Hyalomma*. Common vectors include *H. anatolicum anatolicum*, *H. detritum* and *H. asiaticum*. Tropical theileriosis is a milder disease than ECF and has a much lower mortality in cattle. However, it is an economically important impediment to livestock improvement. In enzootic areas, *Bos taurus* cattle can have a mortality of 40–80%, and *Bos indicus* cattle, which are more resistant to *T. annulata*, can have as much as 20% mortality, mostly in calves. Symptoms include fever, swollen lymph glands, weight loss, anorexia, and apathy. A generalized leucocytosis occurs with great reduction in RBCs, resulting in hemolytic anemia. Organs that are damaged are mostly similar to those damaged in East Coast Fever. Erythrocytic schizogony is common in the life cycle of *T. annulata*. Cattle that survive the disease develop a persistent immunity.

Several species of *Theileria* infect small ruminants. *Theileria hirci* occurs in eastern and southern Europe, the Near and Middle East and in northern Africa. It is transmitted by *Hyalomma anatolicum*. It produces a disease that is highly pathogenic in sheep and goats. *Theileria separata*, a non pathogenic parasite of sheep, is found in Tanzania and is transmitted by *Ripicephalus evertsi*. *Theileria ovis* is worldwide in distribution and is transmitted by many different ticks, including species of *Ornithodorus*, *Hyalomma*, *Haemaphysalis*, *Dermacentor* and *Rhipicephalus*. It produces a disease with little or no pathogenicity in sheep and goats.

Wild and domestic cats are infected by *Theileria felis*, which causes feline cytauxzoonosis in the United States. It is transmitted by *Dermacentor variabilis*. The disease can be fatal unless treated. Cougars and bobcats are carriers of the disease, but show no symptoms.

► Ticks

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Pistachio Seed Wasps

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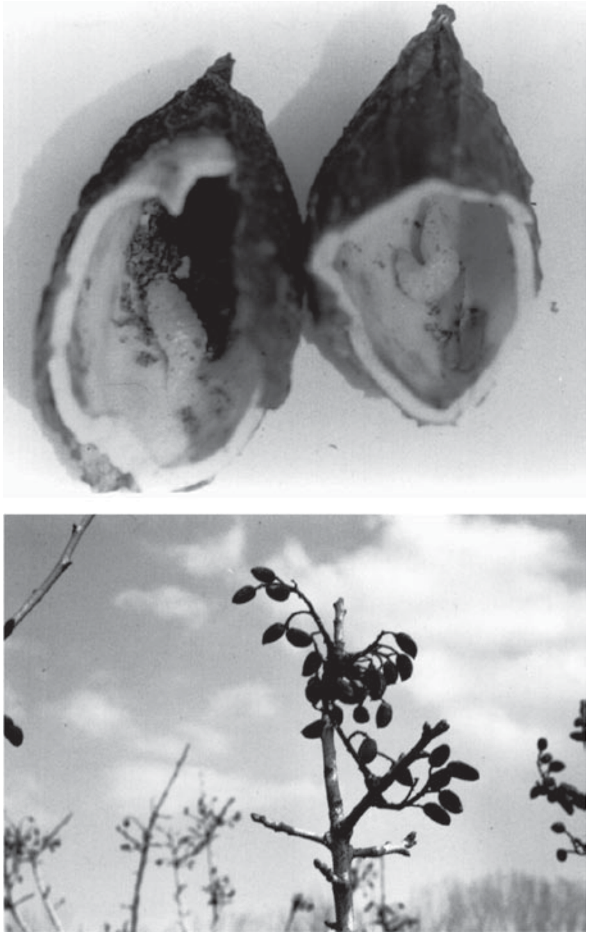
Two species of such wasps are known pests of pistachio because they destroy the fruit. They belong to different families of the Hymenoptera, and their population densities vary with the region and with time. In some orchards the two species co-exist, but one of them usually outnumbers the other. In addition to fruits of the cultivated pistachio, *Pistacia vera*, both these wasps infest also fruits of *P. terebinthus*.

Eurytoma plotnikovi Nikol' Skaya (Eurytomidae)

The adult female is 4–5 mm long and has a reddish brown head and thorax, yellowish red abdomen and red eyes. The legs and the two basal antennal articles may have a lighter color, but this varies with the region. The antennae have ten segments, with the basal one, the scape, being three times as long as the next one. The male is usually black and a little shorter than the female. The larva is whitish, tapering in both ends, apodous, curved, and is 6 mm in length when fully grown. It occurs from the Mediterranean region east to central Asia.

This wasp is univoltine. However, some individuals may complete their life cycle in 2 years because of prolonged diapause. It overwinters as a fully-grown larva inside the fruit, whether the infested fruit remains on the tree throughout winter or has fallen to the ground. Pupation occurs also inside the fruit, sometime in May, and the adult emerges in late May to late June, after boring an exit hole in the fruit with its mandibles. Oviposition occurs in June. Using her ovipositor, the female inserts her egg near the tip of the fruit. The stalked egg is usually placed on the inner wall of the endocarp. The oviposition hole darkens, is easily seen, and may offer entry to plant pathogenic fungi. The larva (Fig. 64) first feeds on the still tender inner layers of the endocarp, and later, in July to August, on the seed, which it consumes completely or almost so. There it remains in diapause until the following spring. In coastal northern Greece, diapause is terminated between early April and early May, with high temperatures and long days leading to diapause termination. The infested fruits become mummified, and as a rule remain on the tree after the leaves have fallen in autumn. Yet, if the fruits are also infected by a fungus, they mostly drop to the ground, usually in autumn.



Pistachio Seed Wasps, Figure 64 **Fully-grown larvae of *E. plotnikovi* within infested mummified pistachios (*above*), and infested mummified fruits remaining on the tree after harvest (*below*).**

This seed wasp is among the most destructive pests of pistachio in many countries. Thus, control measures are generally needed. One such measure is the collection and destruction of all mummified fruits, whether they are on the tree or the ground. This measure to be effective should be applied by all neighboring growers. If fruit collection in a given area cannot be practiced, one or two insecticidal sprays are needed. The insecticide should preferably be systemic, but contact ones of long residual action also proved effective. The proper time is determined by following the exit of adult wasps from infested fruits kept in cages in the orchard. In Cyprus, a spray applied 3 days after the exit of the first wasps from caged fruits, gave satisfactory protection of the crop.

Megastigmus pistaciae Walker (Torymidae)

The adult female has a golden yellow body, with grey-yellow head, red eyes and reddish reflections on the abdomen. Its length is variable, from 3 to 5.5 or even 6 mm. The front wings have a dark oval spot near the costa. The male is reddish yellow. Males are rare. The larva is grayish white, apodous, curved, narrower in both ends and 6 mm long when fully grown. It occurs in southern Europe, northern Africa, the Black Sea coast, the Middle East, Iran, Central Asia, and the United States.

Oviposition takes place in the fruit and the larva consumes the seed, much like *Eurytoma plotnikovi*, above. In Iran and Tunisia it is reported to be bivoltine. It overwinters as a larva inside the pistachio seeds, pupates in spring, and emerges as an adult in spring or early summer. In Tunisia, the adults of the second generation are seen in April-June, and those of the first in July to August. Overwintering larvae are produced from eggs of both generations. In Iran, adults emerge in mid-April to late May and in mid-June and oviposit shortly before the endocarp is completely hardened.

In California, in addition to pistachios, this wasp often infests the seeds of *Pistacia chinensis*, a common ornamental, as well as fruits of other plants of the same genus. Adult trapping and emergence records indicate two generations per year, with adults being active in June and August to September. Yet, adults emerging during the second period are evidently unable to oviposit through the endocarp which is already hard. Therefore, it is possible that only one generation develops in pistachios in California. This is supported by the fact that a high percentage of larvae of the first generation enter diapause, to give adults in the following spring. A possible second generation may develop in fruits of other species of *Pistacia* having an endocarp that hardens later than that of pistachio.

Damage is similar to that by *E. plotnikovi* and, when it reaches economic levels, control should be applied in spring against the adults. Careful collection and destruction of the fruits housing the diapausing larvae are also effective, if applied by all the growers of a given area, and provided that no other species of host trees are in the vicinity.

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Pit Scales

Members of the family Asterolecaniidae, superfamily Coccoidae (order Hemiptera).

► Bugs

Plague: Biology and Epidemiology

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Plague, also called the black death, is an infectious bacterial disease of humans caused by *Yersinia* (*Pasteurella*) *pestis*. The bacterium is a non-motile, gram negative, plump coccobacillus that is transmitted through the bite of the rat flea, *Xenopsylla cheopis,* from susceptible rat hosts, primarily the domestic rat, *Rattus rattus*. People may sometimes become infected by handling other rodents such as prairie dogs that have sylvatic plague and harbor the infected fleas. The infected rodent populations are often decimated by the disease and the hungry fleas abandon the host carcasses in search of new hosts, often domestic rats, cats or even humans. Direct bacterial infection can occur in humans who handle dead rodents or who care for infected domestic cats. In such cases, the bacterium may enter an open wound. Airborne bacterium in the cough of an infected cat or human can also be the source of infection (pneumonic plague).

In the Middle Ages, plague killed millions of people in Europe and, from 1924 to 1925, there was an urban plague epidemic in Los Angeles. Since 1974, small scattered foci of the plague were identified in northern regions of China and other Asian countries, Southern Africa and Madagascar, and in Brazil. In the United States, between 1970 and 1998, small foci have been confined to rural areas of Arizona, California, Colorado, and New Mexico with 36 or as many as 191 cases reported from each of these regions.

Plague induces three types of clinical pathologies in human hosts: the bubonic, primary pneumonic, and primary septicemic plague. Of these, the bubonic plague is the most common and is caused by the bite of an infected flea. Within 2–4 days of infection the person experiences chills, high fever, headache, nausea, and vomiting. There is also evidence of rapid pulse and rapid breathing accompanied by anxiety. Physiologically, the neutrophile leukocyte counts are rapidly elevated. Concomitant with these symptoms, single or multiple enlarged hemorrhagic lymph nodes, the "bubo" (hence the name bubonic plague), appear and are painful and tender. If treated early with antibiotics such as streptomycin, gentamicin, tetracycline, or chloramphenicol, the infection is often eliminated. However, if treatment is delayed, death ensues within 24 h as a result of toxemia even though the bacteria are killed by the antibiotic. About one in seven patients in the United States dies from the disease. Mild variations of the disease (plague minor) may occur and involve minimal toxemia with small "buboes" which contain evidence of the bacterium (thus resulting in the diagnosis). However, these patients frequently survive. Other patients may serve as "carriers" with temporary bacterial infection in the throat (transient pharyngeal carrier) but who may have no manifestations of the disease.

Patients with primary septicemic plague may occur in about 1% of cases. The disease pathogenesis is not as clear-cut as in bubonic plague infections. Sudden fever, meningitis, hemorrhage and pneumonia are common. Presumably, the infection is induced by direct introduction of the bacillin into a blood vessel.

Primary pneumonic plague is contracted by inhalation of the bacterium in aerosol form from coughing patients, and from airborne bacilli released from the remains of infected people or animal carcasses. There is a 48–60 h incubation period, followed by sudden chills and fever. The sputum and other body exhudates of persons with primary pneumonic plague are replete with *Y. pestis* bacilli but the individual exhibits no symptoms of pneumonia. Death occurs within one or two days after infection, as a result of respiratory distress and toxic shock.

The vector of the bacterium, the (Oriental) rat flea, *Xenopsylla cheopis*, like other fleas, belongs to the insect Order Siphonaptera. Unlike most other insects, fleas have a bilaterally flattened body and possess jumping legs than enable them to jump more than 100 times their body length, and even to heights of more than 30 cm. They have piercing-sucking mouthparts that enable them to pierce the skin of their rodent or human host and siphon the blood. The proteins in the blood are important for flea egg development. Fleas have a holometabolous form of development involving an egg, larval and pupal stages, and the adult male and female.

The eggs (about 0.5 mm long) do not adhere to the rat's body but usually fall off into the nest. After 2–21 days, depending on temperature, one larva hatches/egg and feeds upon the detritus and flea feces. There are three larval instars that require 9–15 days to reach the pupal stage. Larvae have a somewhat cylindrical body, have no legs or other appendages, and are covered with long setae. They have chewing mouthparts. A mature larva may measure up to 4 mm long. The pupal stage lasts 5–7 days but can be prolonged if temperatures are low. The pupa may spin a silken cocoon around itself. Adults may live for 38–100 days, depending on the humidity. Such longevity has epidemiological implications, particularly in relation to plague as they may allow the pathogen to survive long after an outbreak has been though to be eliminated.

Several public health and environmental management strategies have been established in the United States to prevent plague infections. These involve sanitation measures to reduce rodent infestations where people work, securing grain and other food storage areas from rodent entry, use of rodenticides in areas (e.g., ships and docks) where rodents may breed, and applying insecticides to kill fleas, particularly in rodent nests where flea eggs, larvae, or pupae may be sequestered.

► Fleas
► History and Insects

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Planidiiform Larva

A flattened body form found in the active first instar of certain parasitoids in the orders Diptera and Hymenoptera. This mobile stage, occurring before the insect penetrates the host, is called a planidium (pl., planidia).

Planidium

In certain insects that undergo hypermetamorphosis, the first instar larva, which is legless and somewhat flattened. This is found in certain Diptera and Hymenoptera (contrast with triungulin).

Planta (pl., plantae)

The basal joint of the posterior tarsus in pollen-gathering Hymenoptera.

Plant Bugs (Hemiptera: Miridae)

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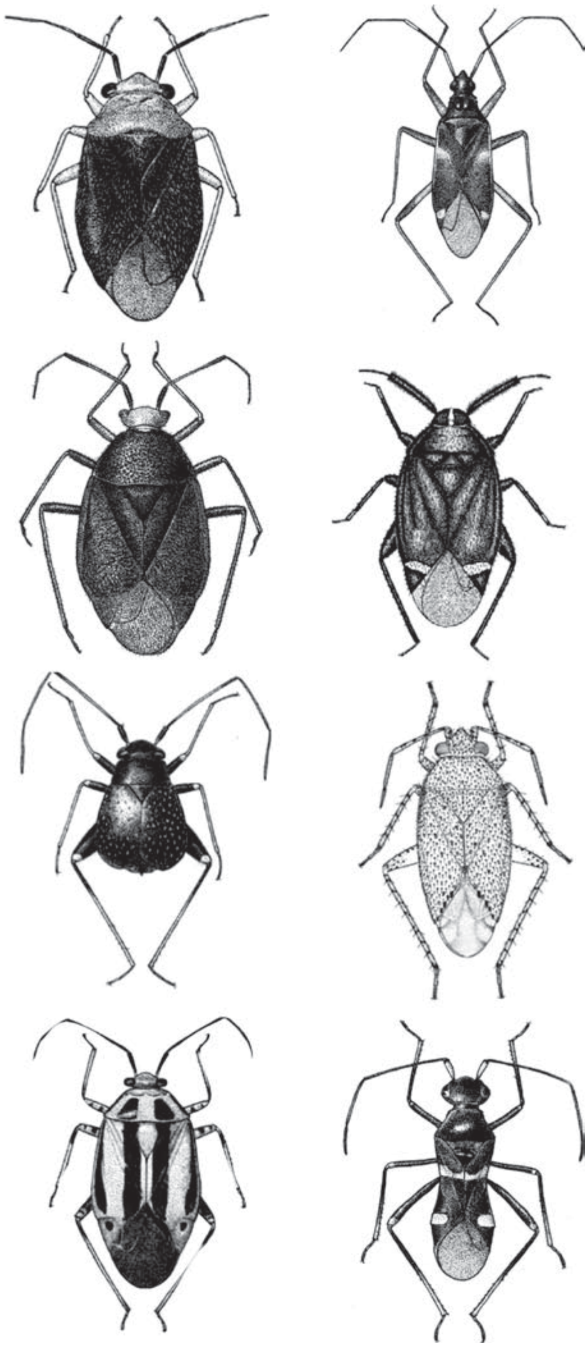
The family Miridae, often referred to as plant bugs, is the largest true bug family. Worldwide, more than 10,000 species of Miridae are known, but this number is expected to more than double once the tropical faunas are more thoroughly studied. Plant bugs belong to the superfamily Miroidea, infraorder Cimicomorpha, and suborder Heteroptera, within the order Hemiptera. Also included in Miroidea are the families Joppeicidae, Microphysidae, Thaumastocoridae, and Tingidae.

Eight mirid subfamilies are currently recognized (Fig. 65), primarily on the basis of pretarsal structures and male genitalia. Mirinae is by far the largest subfamily, followed in size by Phylinae, Orthotylinae, Bryocorinae, Deraeocorinae, Cylapinae, Isometopinae, and Psallopinae. Mirinae are characterized largely by the apically divergent parempodia on the claws and male genitalia with an inflatable aedeagal membrane; Phylinae, by hairlike or setiform parempodia and straplike male genitalia; Orthotylinae, by apically convergent parempodia, unique secondary gonopore, and frequently complex vesica and parameres; Bryocorinae, by the often stout mouthparts and tarsi, frequently single-celled hemelytral membrane, and fleshy pseudopulvilli on the claws; Deraeocorinae, by the basally toothed claws and generally punctate pronotum and hemelytra; Cylapinae, by the apically notched claws, setiform parempodia, long slender antennae and legs, and often stylate eyes; Isometopinae, by the setiform parempodia, often apically toothed claws, two-segmented tarsi, plesiomorphic ocelli, strongly modified head, and single-celled hemelytral membrane; and Psallopinae, by setiform parempodia, apically toothed claws, two-segmented tarsi, head structure, and single-celled hemelytral membrane.

Morphology

Adults range in size from 1.5 mm or less in some bryocorines, orthotylines, and phylines to more than 15 mm in certain restheniine Mirinae. Plant



Plant Bugs (Hemiptera: Miridae), Figure 65 **Some plant bugs: (*top row left*) the yucca plant bug, *Halticotoma valida* (Bryocorinae): 3.0–3.5 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*top row right*) *Fulvius imbecilis* (Cylapinae): 4.00 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*second row left*) *Bothynotus modestus* (Deraeocorinae): 5.0 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*second row right*) *Myiomma cixiiforme* (Isometopinae): 3.00 mm long. North America (by Thomas J. Henry, courtesy of the U.S. Department of Agriculture); (*third row left*) the garden fleahopper, *Halticus bractatus* (Orthotylinae): 1.5–2.0 mm long. North, Central, and South America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*third row right*) the cotton fleahopper, *Pseudatomoscelis seriata* (Phylinae): 3.0–3.5 mm long. North and Central America, West Indies (by Linda H. Lawrence, courtesy of the U.S. Department of Agriculture); (*bottom row left*) the fourlined plant bug, *Poecilocapsus lineatus* (Mirinae): 7.0–7.5 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*bottom row right*) *Sericophanes heidemanni* (Orthotylinae): 3.0–3.5 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution).**

bugs can be described as delicate and are well known for their tendency to lose appendages when preserved in alcohol. Many Miridae often are brightly colored, ranging from bright, shiny yellow to vivid orange or red and black. Others are more cryptically colored green, gray, brown, or black, closely resembling leaves, stems, flowers, and bark of their hosts. Mirids may be nearly glabrous or may possess diverse kinds of setae, ranging from simple and hairlike to thick and woolly, silky, or even flattened and scalelike.

The family is characterized by a four-segmented antenna, four-segmented labium, primarily three-segmented tarsi (only two segments in Isometopinae, Psallopinae, and some Bryocorinae and Cylapinae); declivent to porrect head, lacking ocelli (except in Isometopinae); trapeziform pronotum, often bearing paired callosities or swellings on the anterior half; paired lateroventral scent glands on the metathorax; and asymmetrical male parameres or clasping structures. Miridae have two pairs of wings, the characteristic hemelytra or forewings, and shorter, membranous hind wings. The hemelytron of fully winged or macropterous Miridae possesses a triangular-shaped cuneus, one or two closed cells on the apical membrane, and a widened costal area frequently referred as the embolium. Miridae can also have varying degrees of hemelytral short wingedness or brachyptery, ranging from only a reduced apical membrane to the absence of even wing stubs. Some taxa exhibit beetlelike (coleopteroid) hemelytral modifications. While brachyptery can be exhibited by either sex, it occurs most often in females. Myrmecomorphy, or a resemblance to ants, is a common adaptation in many groups, generally characterized by a rounded head well separated from a sometimes anteriorly narrowed pronotum, and constricted hemelytra (or a basally constricted abdomen in brachypterous forms) to give the image of three antlike body sections.

Mirid eggs, sometimes described as banana- or cigar-shaped, are elongate and slender, straight to weakly curved, and generally 0.6–2.5 mm long. They are typically creamy or white. The egg shell or chorion usually is smooth but may bear faint hexagonal sculpturing. A characteristic operculum or egg cap, bearing two micropyles, is always present. Eggs frequently are inserted singly but can be laid in groups of 2 or 3 to 20 or more on their host and usually are deposited deep within leaf or stem tissue, within structures such as lenticels, or tucked tightly within leaf bundles or sheaths of grasses and other plants. The operculum usually remains visible and flush with the surrounding tissue until eclosion.

Nymphs or larvae (as they often are called outside the U.S.) undergo gradual or paurometabolous metamorphosis. Nymphs resemble adults in general appearance, differing primarily in body proportions (particularly the head, thorax, and appendages), pigmentation, two-segmented tarsi, and the lack of wings and reproductive structures. Each instar possesses a characteristic dorsal abdominal scent gland, the opening of which is visible between abdominal terga III and IV. All but a few species undergo five stages. Instars I and II lack wing pads and the meso- and metanotal segments are of nearly equal length; traces of wing pads appear in instar III, with the metanotum becoming wider than the mesonotum; larger wing pads extending onto the abdomen develop on the metanotum in instar IV; and fully developed pads extending well onto the abdomen are present in instar V. The ovipositor in females or the genital capsule of males sometimes are visible through the cuticle in fifth instars, but are not functional until the adult stage.

Habitats and Host Plants

As the common name "plant bugs" suggests, mirids are mainly plant inhabitants. Though often underappreciated for their species richness, they are among the most common insects found on herbs, shrubs, and trees. Plant bugs are common not only in managed systems and ruderal sites such as vacant lots but also in specialized communities such as granite outcrops, pine barrens, serpentine barrens, and shale barrens. They can be found from below sea level to an altitude of nearly 5,400 m.

Mirids develop principally on coniferous gymnosperms and dicotyledonous and monocotyledonous angiosperms. Twenty or more mirid species can be found on a single species of oak or pine. In arid regions of the southwestern United States and Mexico, shrubs such as ephedra (*Ephedra*), mesquite (*Prosopis*), rabbit-brush (*Chrysothamnus*), sagebrush (*Artemisia*), and saltbush (*Atriplex*) also are characterized by a diverse plant bug fauna. Some shrub- and tree-inhabiting Miridae are most numerous on isolated plants, in hedgerows, or along forest edges. Other species prefer shaded habitats or are shade tolerant. A few species are associated with fungi, especially those that grow on logs and tree trunks. The first moss-feeding plant bug was recently described from Japan. While no mirids are truly aquatic, those species that live on plants in or on the edge of water, such as water-hyacinth, might be considered semiaquatic. The Miridae also include species that are found in the litter layer, in ant nests, and in webs of subsocial spiders.

The Miridae are mostly a host-restricted group. Diet breadth ranges from strict monophagy, feeding only on one plant species, to polyphagy. Among well-known generalists are the European tarnished plant bug (*Lygus rugulipennis*) in Eurasia and the tarnished plant bug (*L. lineolaris*) in North America. Even large, agriculturally important genera such as *Lygus*, which tend to be dominated by broadly polyphagous species, usually contain specialists of narrow host range. Although predatory mirids typically show broader host associations than do plant feeders, species of mainly predacious genera, such as *Deraeocoris* and *Phytocoris*, often develop only on one plant genus (e.g., pine or oak).

Life History and Habits

In temperate regions, most mirids that feed on woody plants overwinter as eggs inserted into various plant parts or in crevices on the host. In spring, the hatching of diapausing eggs often is synchronized with budbreak of host plants and is triggered by water uptake of the host. Plant bugs that feed on trees and shrubs tend to produce only one annual generation – that is, populations are univoltine. Overwintering in the adult stage is typical of multivoltine species found on herbaceous weeds, including grasses, and field crops. Among other plant bugs overwintering as adults are some species of the predacious genus *Deraeocoris*.

Nymphal development, which generally is inversely proportional to temperature, can be completed in 12–35 days, depending on the species, temperature, and diet. Males of many species emerge slightly earlier than females (i.e., exhibit protandry). A sex pheromone released by the female attracts the male in certain species of the subfamilies Bryocorinae, Mirinae, and Phylinae. Olfactory receptors on the antennae allow males to detect the female pheromones. After a short premating period (usually only several days), mating takes place on the host plant. Elaborate courtship behavior may or may not be involved, depending on the species. Multiple matings apparently are common. In many species, mated females deposit about 30–100 eggs, but fecundity can be lower or as high as several hundred eggs. The insertion of eggs into host tissue, referred to as endophytic, reduces water loss, minimizes winter mortality, and provides some protection from natural enemies. As noted above, endophytic oviposition also is important in establishing contact with the host's vascular system so that egg hatch of plant-feeding species can be synchronized with host phenology.

Eggs of plant bugs are moved readily in shipments of nursery stock; the usually inconspicuous eggs are unlikely to be detected by plant-regulatory inspectors. Consequently, numerous Old World mirids have been accidentally introduced into North America and have become established in the Nearctic fauna.

Plant-feeding mirids generally use high-nitrogen resources, including buds, meristems, young leaves, pollen, and ovules. Most plant bugs are mesophyll rather than vascular-tissue feeders. Phytophagous members of the family, as feeders on liquefied solids, should not be considered sap feeders. Predatory mirids also suck up liquefied solids. Mirids have been described as lacerate (or macerate) and flush feeders. Their flexible stylets (paired maxillae and mandibles) macerate mesophyll cells, or prey tissues in the case of predators, and digestive enzymes from their saliva liquefy plant or animal material so that it can be imbibed through the narrow food canal. Although mirids do not tap into sieve tubes as aphids and certain other phloem-feeding hemipterans do, some species do feed from vascular tissues of their host plants. Adults of both leaf- and flower-feeding species sometimes disperse to other plant species to feed on nectar and pollen.

Mirids probably exhibit greater trophic plasticity than bugs of any other hemipteran family. Even important plant pests such as lygus bugs can be scavengers and facultative predators. Other plant bugs are mostly or entirely predacious. Predatory species range from multivoltine generalists that during the season track various prey over a wide range of host plants to univoltine specialists that feed only on a certain type of prey on a particular plant genus. Thus, some mirids prey only on oak-infesting scale insects, whereas others specialize on thrips or lace bugs.

Economic Importance

The Miridae sometimes are stated to be important vectors of plant pathogens. Although some species help disseminate fungal and bacterial pathogens, plant bugs are not among the principal vectors of plant viruses. The bugs' destruction of plant cells presumably makes it difficult for obligate parasites to infect the host plant, and their salivary secretions might inactivate plant viruses. Moreover, as mesophyll feeders, mirids would not be expected to vector phloem-limited viruses.

Mirids, however, are significant pests of numerous crops, including alfalfa, apple, cocoa, coffee, cotton, guava, peach, sorghum, strawberry, sugar beet, and tea. Symptoms of plant bug injury range from foliar chlorosis, crinkling, and shot holing to lesions, cankers, and abnormal growth patterns such as stunting, bushiness, multiple leadering, and witches'-brooming. Because symptoms of mirid feeding can be so similar to those caused by abiotic factors, as well as by other insects and plant pathogens such as fungi, bacteria, and viruses, their injury often is misdiagnosed.

Millions of dollars are spent each year in attempts to control lygus bugs and other mirids that affect cotton production in the United States. An intensive, and sometimes excessive, use of insecticides against cotton-infesting plant bugs has led not only to outbreaks of secondary pest species but also the development of insecticide tolerance or resistance among mirid populations. Certain species of the subfamily Bryocorinae, which are key pests that limit the production of cocoa in West Africa, also have developed resistance to chlorinated hydrocarbon insecticides.

The agricultural importance of plant bugs also extends to predacious species. Some of the most successful examples of long-term biological control involve the use of Miridae that feed on eggs of delphacid planthoppers. For example, the introduction into Hawaii of a mirid (*Tytthus mundulus*) from Australia has been credited with saving the Hawaiian sugar cane industry from an exotic pest, the sugarcane delphacid. Another case of successful classical biological control involves a non-native predatory plant bug that preys on an introduced planthopper that attacks taro in Hawaii. Other predacious mirids help suppress populations of rice-infesting planthoppers. Numerous crops benefit from native species of Miridae that prey on mites, thrips, leafhoppers, psyllids, whiteflies, scale insects, aphids, lace bugs, and the eggs, larvae, and pupae of various beetles, flies, and moths. These naturally occurring predators should be conserved in pest management programs. Since the 1980s, dicyphine Bryocorinae have been studied and used successfully against thrips, whiteflies, and aphids that are pests of greenhouse crops.

In addition, some mirids penetrate mummified aphids, killing the larvae, prepupae, or pupae of the parasitic wasp within the mummies. Plant bugs sometimes also prey on various life stages of insects intentionally released as biological control agents of weeds. Mirids might impair the effectiveness of parasitic wasps that are enemies of crop-infesting aphids and herbivores released for the biological control of weeds, but the potential detrimental effect of such predation on population dynamics of the prey species is unknown.

Natural Enemies

In all their life stages, mirids are subject to attack by a diversity of predators, parasitoids, and microbial pathogens. Among vertebrate enemies are lizards, frogs, toads, and birds. An even more diverse group of invertebrate predators helps suppress plant bug numbers. Generalist predators include spiders, big-eyed bugs (geocorids), damsel bugs (nabids), minute pirate or flower bugs (anthocorids), assassin bugs (reduviids), mantids, and ants. Well-known families such as lady beetles (coccinellids) and flower flies (syrphids) include predators of mirids, but members of these groups are unimportant natural enemies of plant bugs. Despite being partially or completely concealed in crevices or plant tissues, the eggs of mirids are killed by parasitic wasps. The most important egg parasitoids belong to the family Mymaridae. Mirid nymphs are killed by wasps of the family Braconidae, specifically certain specialized parasitoids of the subfamily Euphorinae. At times, euphorine braconids cause population crashes of injurious mirids.

Other biotic agents that can limit plant bug populations are parasitic nematodes (mermithids) and various microbial pathogens. Fungi are more important natural enemies of mirids than are bacteria or protozoa. Laboratory cultures, however, can be decimated by bacteria and microsporidian protozoa. No virus diseases of mirids are known.

► Bugs (Hemiptera)

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Plant Compensation

Feeding by insects does not always result in less productivity of plants, due to compensatory physiological processes in the injured plant. Insect feeding can actually stimulate a plant to grow more than an uninjured plant, but more often results in partial compensation for the removed plant tissue, resulting in less damage than expected. Compensatory processes function best at low levels of damage, and are due to such factors as removal of apical dominance, removal of less productive tissue, increased penetration by light, and reduction in carbohydrate-induced inhibition of photosynthesis.

Plant Extrafloral Nectaries

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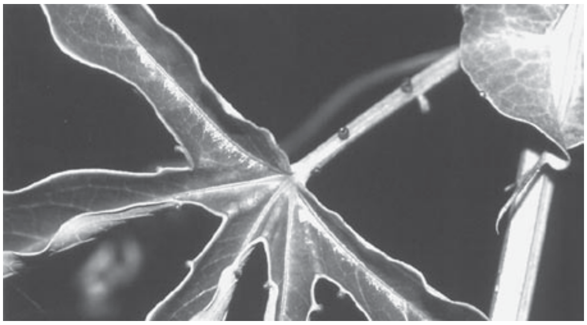
It is well known that plant flowers produce nectar that is important in encouraging pollination, as well as providing food for bats, birds and insects (Fig. 66). However, few people are aware of plant extrafloral nectaries that are nectar-producing glands physically apart from the flower. Extrafloral nectaries have been identified in more than 2,000 plant species in more than 64 families. For example, in nine cerrado areas of Brazil's São Paulo and Mato Grosso states, the plant families Mimosaceae, Bignoniaceae and Vochysiaceae contained the highest frequency of extrafloral nectaries.

Several review articles dealing with extrafloral nectaries or related ecological relationships and at least one book is available. In this article we briefly summarize some aspects of current knowledge about plant extrafloral nectaries and discuss their role and significance to parasitic and predatory arthropods that are important biological control agents.

Extrafloral nectaries were distinguished from floral nectaries in 1762. In 1874 Delpino described extra-nuptial nectary glands. Studies of extrafloral nectaries on plants from various families and habitats provide data on the location, morphology, and abundance of extrafloral nectaries. Approximately 93 angiosperm families with 2,000 species have extrafloral nectaries, but monocotyledons have few taxa with extrafloral nectaries. Plants with extrafloral nectaries tend to be woody and perennial. Extrafloral nectaries are often found on plant species that grow as vines (Fig. 67). Aquatic plants appear to be entirely devoid of extrafloral nectaries. The presence or absence of extrafloral nectaries may vary even among closely related species or cultivars. Whereas up to 80% of plants in tropical habitats have extrafloral nectaries, the proportion of plants in temperate climates varies widely. Only 14% of plants sampled in Nebraska had extrafloral nectaries. In plant communities similar to those of Nebraska, no plants in northern California were found to have extrafloral nectaries. The percent of plant cover with extrafloral nectaries in a myriad of habitats varies from 0 to 80%. Plants with extrafloral nectaries are few in number in areas that do not have ants. For example, at higher elevations in Jamaica in comparison to sea level habitats, ants and plants with extrafloral nectaries were significantly lower. Hawaii is an excellent example with few species of native plants with extrafloral nectaries. Extrafloral nectaries often occur on plants noted for toxicity, thorns, or coriaceous leaves. An interesting model predicting the probability of development of mutualistic associations among plants and ants indicates a probability of 1.0 when ants are "omnipresent" and predicts only low probability when ants are few, and then only under very narrow conditions.

Plant Extrafloral Nectaries, Figure 66 **Ants frequently visit the nectaries of the vine *Smilax* sp.**



Plant Extrafloral Nectaries, Figure 67 **The knob-shaped extrafloral nectaries of the passion vine, *Passiflora* sp.**

Some Plant Families with Extrafloral Nectaries

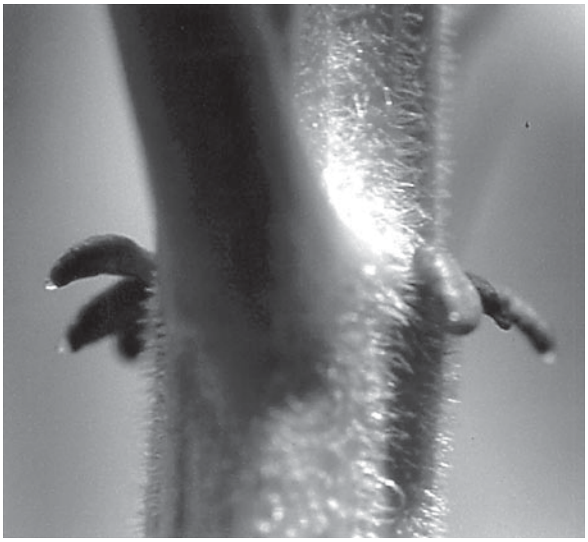
- Asclepiadaceae
- Bignoniaceae
- Caesalpiniaceae
- Caprifoliaceae
- Compositae
- Convolvulaceae
- Curbubitaceae
- Euphorbiaceae
- Fabaceae
- Leguminaceae
- Liliaceae
- Malvaceae
- Mimosaceae
- Papilionaceae
- Rosaceae
- Salicaceae

Location and Morphology

Extrafloral nectary glands may be located on leaf laminae, petioles, rachids, bracts, stipules, pedicels, fruit, and most any above ground plant parts. Their size, shape and secretions vary with plant taxa. Extrafloral nectaries on Nebraska plants are most common (73%) on the foliage. Elderberry, *Sambucus nigra*, extrafloral nectaries (Figs. 68 and 69) are stalk-like on the base of leaves with nectar-producing tissue on top with a single central vascular bundle of dense cytoplasm with a well-developed endoplasmic reticulum. Light microscopy shows that very young nonsecreting nectaries are less than 2 mm, still-growing nectaries with nectar droplets are 2–4 mm and full-grown nectaries are 5–6 mm with small vacuoles fused to large vacuoles.

Apocynaceae, for example *Nerium odorum* L., have extrafloral nectaries on the adaxial surface at the junction of petiole and lamina with short apices, one or two to six to seven nonvascular nectaries develop on each leaf axial. These nectaries are active on young leaves and dry on mature leaves. *Ipomoea carnea* has

Plant Extrafloral Nectaries, Figure 68 **Ants frequently visit the large extrafloral nectaries of the elderberry, *Sambucus* sp.**



Plant Extrafloral Nectaries, Figure 69 **The large extrafloral nectaries of the elderberry, *Sambucus* sp., produce large droplets of nectar.**

two types of extrafloral nectaries with one set of two located on the distal end of the petiole. These mature before the lumina. The other set of five in a ring is on the pedicel which develop with flower buds. Nectar is produced continuously with no change in rate. *Rincinus communis* has extrafloral nectaries found on the lower side of petioles and at the base of leaves with normally three to seven per leaf. Nearly all *Prunus* spp. have extrafloral nectaries, notable exceptions include the low-chill peach, *P. persica*, cultivars "JunePrince" and "GoldPrince" developed by commercial breeding programs. Peach nectaries are globose or reniform and located on the leaf petioles. Cherry laurel, *P. laurocerasus* L., has histoid extrafloral nectaries on the lower leaf surfaces. *Calotropis gigantea* and *Wattakaka volubilis* (Asclepiadaceae) have multiple nectaries at the junction of the petiole and lamina. *Cipadessa baccifera* (Roth.) (Meliaceae) have 25–35 extrafloral nectaries per leaf. The nectaries occur mostly on the abaxial surface of the rachis. Magnified, the extrafloral nectaries appear as ridges and are green on immature leaves and reddish brown on mature leaves. The nectaries of the angiosperm, *Pteraduim aqualinum*, are smooth protrusions located on the stipe and frond and consist of vascular tissue with abundant mitochondria with well-developed vacuoles, a large number of plasmodesmita and less dense cytoplasm. Extrafloral nectaries of cotton, *Gossypium hirsutum*, are closely packed papillae in a pyriform depression on the lower midvein of the leaves. Peak secretion of cotton extrafloral nectaries occurs in July. *Passiflora incarnata* has two sets of extrafloral nectaries, one set is located on the glands of the petiole at the base of each leaf and the other set consists of pairs of glandular bodies on each of three bracts directly underneath the flower or bud. *Dioscorea rotundata* has extrafloral nectaries embedded in the leaf lamina with the pore opening on the lower leaf surface. Each gland is closely associated with leaf veins. Vetches have stipular nectaries present on young plants.

Some Species with Extrafloral Nectaries

- *Abutilon* (Indian mallow)
- *Ailanthus altissima* (silk tree)
- *Allamanda nerifolia*
- *Aphelandra* (tropical herb or shrub)
- *Callecarpa* (beauty berry)
- *Campsis radicans* (trumpet creeper)
- *Cassia fasciculatus* (partridge pea)
- *Catalpa speciosa* (Indian bean)
- *Cattleya* (orchids)
- *Cissus rhombifolia* (ivy)
- *Clerodendron* (tube flower)
- *Costus* (spiral ginger)
- *Crotolaria striata*
- Croton
- Curcurbits
- *Dioscorea* sp. (air potato)
- *Fraxinus* sp. (ash)
- *Fritillaria* sp. (N. Am. lily)
- *Gossypium hirsutum* (cotton)
- *Helianthus* sp. (sunflower)
- *Helionthella quinquenervis* (W. N. Am. herb)
- *Hibiscus* sp.
- *Hoya* sp.
- *Impatiens balsamina*
- *Ipomoea pandurata* (morning glory)
- *Osmanthus* sp. (devil weed)
- *Oxypetalum* sp. (S. Am. shrub)
- *Paeonia* sp. (peony)
- *Passiflora incarnata* (passion flower)
- *Pennisetum* sp. (tropical grass)
- *Phaseolus* sp. (beans)
- *Polygonium* sp. (knot, smartweed)
- *Prunus* spp. (peach) most of 431 species have
- *Pteridium aquilinum* (bracken)
- *Ricinus communis* (castor bean)
- *Robinia pseudoacacia* (black locust)
- *Salix* sp. (willow)
- *Sambucus nigra* (elderberry)
- *Smilax macrophylla* (green briar)
- *Thunbergia grandifloria* (blue trumpet vine)
- *Viburnum opalus*, *V. americanum*

- *Vicia sativa* (vetch)
- *Vigna unguiculata* (cowpeas)

The Location of Some Extrafloral Nectaries on the Plant

- *Ailanthus*: leaf margins
- *Allamanda*: leaf axils
- *Callecarpa*: adaxial surface near veins at leaf base
- *Cassia*: petiole
- *Cissus*: stipule
- *Costus*: outer surface of floral bracts
- *Crotalaria*: flower stalk
- Croton: petiole
- Curcurbits: lamina, pendunular bracts, abaxial surface of calyx
- *Fraxinus*: glandular trichomes on lower leaf surface
- *Gossypium*: leaf or flower bracts
- *Helianthus*: flower bracts and phyllaries
- *Hibiscus*: sunken, elongate cavity part of midvein adaxial surface
- *Hoya*: upper leaf surface
- *Impatiens*: petiole and leaves
- *Ipomoea*: lower leaf surface, petiole, pedicel just below junction with sepals
- *Osmanthus*: glandular trichomes on lower leaf surface
- *Passiflora*: petiole, bud and flower bracts
- *Phaseolus*: on the cushion-like compressed lateral branches on the inflorescence axis
- *Prunus*: distal part of leaf petiole/leaf blade, adaxial leaf
- *Pteridium*: stipe and fronds
- *Ricinus*: leaf and inflorescence
- *Robinia*: stipules
- *Salix*: leaves
- *Sambucus*: stipules
- *Smilax*: tiny, flattened on lower leaf surface
- *Thunbergia*: sepals
- *Viburnum*: lower leaf surface near petiole
- *Vicia*: stipules
- *Vigna*: stipules and inflorescence stalk

Composition and Periodicity

The most prevalent components of floral nectar are a combination of fructose, glucose, and sucrose in various proportions with other sugars such as maltose, trehalose, metazelose, methyl-glucose. The content of extrafloral nectaries differs from floral nectar even on the same plant, varies by taxa, and may or may not flow in a daily pattern. The composition of extrafloral nectaries secretion is about 95% sugar – predominantly sucrose, glucose and fructose – with the other 5% consisting of a wide array of amino acids, proteins and other important nutrients. Extrafloral nectar contains significantly higher numbers of amino acids and non-protein amino acids than does floral nectar. All of the common amino acids in floral nectaries are also equally common in extrafloral nectaries. Other components of extrafloral nectaries may include acids, proteins, lipids, and other organic compounds.

Factors which determine the concentration of the nectar solution include proximity of the phloem vessels, proportion of xylem in the vascular trace, photosynthetic rates of associated organs and local climatic conditions. The volume of extrafloral nectar is strongly affected by evaporation. *Ricinus communis*, castor bean, extrafloral nectar is mostly sugars supplied by the phloem, with the xylem supplying some water. The nectar has lower levels of amino acids than the phloem. Cherry laurel has extrafloral nectaries that produce fructose, glucose, saccharose, and 38% dry substances.

Extrafloral nectaries have a longer secretion period than floral nectaries but often do not have a concise diurnal secretion pattern. Studies have shown that the peak secretion of extrafloral nectaries can occur in the morning and the evening or can be relatively constant day and night. Extrafloral nectaries secretion often begins several weeks prior to flowering and may last through the flowering period. The most active extrafloral nectaries usually occur at the same time with and are associated with plant reproductive organs. In temperate zones peak extrafloral nectaries activity occurs during the middle of the growing season, whereas in tropical habitats secretion may occur continuously during the year. Artificial leaf damage to *Macaranga tanarius* L. induced greater flow from extrafloral nectaries for the next 3 days. Jasmonic acid was found to be the induced chemical responsible for the increase in nectar production rate.

Function and Ecological Interactions

Two hypotheses have been presented to explain the function of extrafloral nectaries. One theory holds the function of extrafloral nectaries as one of a purely physiological function enabling plant waste elimination from metabolism. This hypothesis suggests that extrafloral nectaries may serve as "sap valves" to release extra sugars (Fig. 69). The other theory suggests that the function of extrafloral nectaries is one of plant defense. Extrafloral nectaries may attract ants to protect plants against herbivores, may attract pollinators, as defense against ant-hemipteran mutualisms or may attract ants away from florets to protect from nectar thieving and interference with pollination. Of the plant species with extrafloral nectaries that have been studied, most of the results, although not all, have supported the plant defense hypothesis. It is well documented that many insects use extrafloral nectaries and it is easy to observe beneficial insects such as parasitic Hymenoptera and ladybird beetles feeding on extrafloral nectaries. Many species of ants are found in association with plants having extrafloral nectaries and are thought to be manipulated by the plant using its extrafloral nectaries. Removal of extrafloral nectaries from cotton decreased field populations of both phytophagous (60% reduction) and predacious insects (17–35% reduction). Interestingly, a great many species of vines have extrafloral nectaries and the evolution and selection for extrafloral nectaries is hypothesized to occur as a direct result of the ants using the vines as natural pathways into the forest canopy. Sparsity of extrafloral nectaries in Hawaii seems consistent with a plant antiherbivore defense system that does not function in the absence of ants.

There are five ways in which plants may benefit from interactions with ants: (i) ants protect plants against herbivores, (ii) ants prune neighboring plants which promotes growth and survival of host plants, (iii) ants feed plants with essential nutrients, (iv) ants disperse seeds and fruit, and (v) ants pollinate plants. Studies of the mutualism between plants and ants show that mutualistic association may vary with time, habitat, aggressiveness of ants, and the ability of herbivores to overcome ant predation. Mutualism is favored when the investment in nectar and nectaries is low with high herbivore damage, effective alternative defenses are not

Plant Extrafloral Nectaries, Figure 70 The introduced ladybird, *Harmonia axyridis*, feeds from the extrafloral nectaries of the elderberry, *Sambucus* sp.

available, and effective defenses are provided by ants. For mutualism using extrafloral nectaries to be favored, ants must be omnipresent. However, direct predation by ants may be unnecessary; the mere presence of the ants may be enough. In order for ants to truly be considered as “protectors” of plants they must have the characteristics of aggressive behavior against feeding herbivores, daily activity patterns to provide 24-h protection, actively forage for a plants herbivores, actively forage in large numbers, have nest locations in close proximity to the extrafloral nectaries plant and be able to move (nest mobility) the nest close to extrafloral nectaries plants.

Passiflora incarnata has two sets of extrafloral nectaries. These extrafloral nectaries are visited by five species of ants and the number of ants was correlated positively with the number of extrafloral nectaries and negatively with herbivores. The number of fruit produced was greater on plants with extrafloral nectaries than without. Studies on *Cassia* sp. showed that ant visitation resulted in decreased herbivore numbers and leaf loss with increased growth but did not result in seed set differences. Continuous production of nectar is necessary to attract ants and ant activity follows the secretion patterns of extrafloral nectaries. This continuous production is evident in extrafloral nectaries, but not floral nectaries.

While ant visitation does not affect the reproductive output of plants, it is advantageous if ants protect plants during growth because pollinators are increased by large floral display, and a surplus of initial fruit and seeds may allow a plant to selectively abort genetically inferior progeny. Another way extrafloral nectaries may function is to protect plants against ant-hemipteran mutualism. By supplying nectar to ants, extrafloral nectaries distract the ants from the honeydew produced by the Hemiptera, and the plant incurs less hemipteran damage. Plant antiherbivore mechanisms are often reduced in commercial crops.

The evolution of nectar rewards may illustrate a correlation between plants and ants that provides a consistent plant defense system. The plant may select for biological control by ant protection which probably reduces the potential of damage by herbivores resistant to chemical or structural barriers provided by the plant. Natural selection may operate to optimize the production of nectar from extrafloral nectaries, balancing the cost for production with benefit in leaf and fruit production. A model for facultative mutualism predicts a positive correlation between extrafloral nectaries and ant abundance. Extrafloral nectaries selection is stronger for species that encounter ants frequently. Extrafloral nectaries are expected to be more abundant in vines and may be favored in seasonal environments. Extrafloral nectaries may result in ant symbiosis, not cause it. In Nebraska the occurrence of ants was not related to the distribution of plants with extrafloral nectaries.

Extrafloral nectaries may also function to attract ants to plants which use the ants to disperse seeds. Plants with ants have significantly fewer predators because ants may interfere with predator oviposition. Major herbivorous insects are more likely to be parasitized on plants with high quality nectar that attract parasites. Ants decrease the amount of time *Eurybia* larvae are on inflorescences. Diptera seem more prevalent on *Aerobe* sp.-infested plants.

Ant exclusion studies have shown that removing ants from plants did not lessen the number of ants visiting extrafloral nectaries; however, sugar would not attract ants to plants. Exclusion of ants increased the number of insects on developing capitula but did not affect pollination. *Mentzelia nuda* (Loasaceae), a short wild perennial, has extrafloral nectaries which secrete after flowering, and attract ants, which significantly enhances seed set. The number of ants increases sharply when extrafloral nectar is available, which indicates that ant foragers can respond to a new food source. On black cherry, extrafloral nectaries are most active when ants are most able to prey on herbivores.

Ants visiting extrafloral nectaries may add to an increase in plant fitness by deterring leaf, seed, and flower herbivores and this in turn may increase the number of seeds produced. The defense of plant parts by ants appears to be a flexible interaction using diverse ant species and repelling various types of herbivores. Extrafloral nectaries on flowers may increase parasitoid survivorship, fecundity, retention and pest suppression. In Costa Rica, studies have shown more buds mature to ripe fruit on plants with extrafloral nectaries and a higher ant visitation rate. Ant activity followed the secretion pattern of extrafloral nectaries. Total number of seeds per cyme was significantly higher on plants with ants.

While ants are the most common visitors to extrafloral nectaries, and 30 species of ants have been observed visiting *Passiflora*, extrafloral nectaries are attractive to many families of arthropods. Over an 8-day period, 3,941 insects, including 40 families, 77 genera, and 100 species were observed visiting extrafloral nectaries of *I. carnea* in Costa Rica. The insects included Coleoptera (Fig. 70), Hemiptera, Lepidoptera, Neuroptera, Diptera, and Hymenoptera. Extrafloral nectaries on cotton attract parasitoids and increase the retention time and rate of parasitism. Extrafloral nectaries serve as an important supplementary food source of many insects, including predatory mites on cotton during times of stress when usual food sources are scarce, and are an important nutritional source for parasitic Hymenoptera. Even spiders may respond to the presence of extrafloral nectaries as the presence of salticids are known to enhance seed production of *Chamaecrista nictitans* (Caesalpiniaceae). Nineteen genera and 41 species of ladybird beetles, Coccinellidae, have been observed feeding on extrafloral nectaries.

Extrafloral nectaries offer an important supplemental food source for many beneficial insects (and too, to phytophagous insects including some pest species), particularly during extreme weather conditions such as drought and other times of the year when prey are scarce. Extrafloral nectaries may be valuable if not critical components in the ecology of landscapes. Passion flower, *Passiflora* spp., partridge pea, *Cassia* spp., hairy vetch, *Vicia* sp. and elderberry, *Sambucus* spp., are common examples of plants with large extrafloral nectaries on the leaves and/or stems. A great many opportunities exist to further our understanding of extrafloral nectaries as much remains unknown about the important ecological roles extrafloral nectaries may play. Exploiting extrafloral nectaries and other natural ecosystem functions that increase the presence and effect of natural enemies of pests have great potential to help reduce further the need for conventional pest controls in commercial agriculture and urban landscapes.

► Ant-plant Interactions
► Conservation Biological Control

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Planthopper Parasite Moths (Lepidoptera: Epipyropidae)

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Planthopper parasite moths, family Epipyropidae, total 40 described species, with at least another 30 known species awaiting naming. Species are known from all faunal regions, but are most diverse in Australia. Two subfamilies are known: Epipyropinae and Heteropsychinae. The family is in the superfamily Cossoidea (series Limacodiformes)

Planthopper Parasite Moths (Lepidoptera: Epipyropidae), Figure 71 **Example of planthopper parasite moths (Epipyropidae), *Fulgoraecia exigua* (H. Edwards) from Florida, USA.**

in the section Cossina, subsection Cossina, of the division Ditrysia. Adults are minute to small (4–35 mm wingspan), with head scaling mostly roughened; haustellum absent; labial palpi minute; maxillary palpi absent; antennae bipectinate in males and rather conspicuous. Body robust. Wings quadratic and broadly rounded (Fig. 71). Maculation mostly black or dark brown; sometimes with some spots and iridescence. Adults are crepuscular and nocturnal; females are sedentary. Larvae slug-like with rounded dorsum; parasitic on fulgorids and planthoppers (Hemiptera). Eggs are laid on various plants and upon hatching, larvae search for suitable hemipteran hosts to parasitize.

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Planthoppers (Hemiptera: Fulgoroidea)

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Current cladistic and molecular studies are resolving their placement in the Hemiptera and the placement of odd genera and tribes within families. Perhaps only 20% of the species of the superfamily are described.

Order: Hemiptera
Suborder: Fulgoromorpha
Superfamily: Fulgoroidea
Families: 16–21, consensus not yet reached

Morphology

The superfamily is usually identified by the placement of the eyes, antennae, and lateral ocelli on the genae, which are separated from the front of the head by lateral carinae; by the tegula, a small plate covering the base of the wing; a y-shaped claval vein in the forewing; and rows of spines at the apex of the hind tibia and first tarsomere. Specimens measure from 2 mm to 10 cm (4 in.).

Phylogeny

At the moment, but still subject to change, we believe the Sternorrhyncha are the sister group of the rest of the Hemiptera. Next, the Fulgoromorpha (the suborder, which is equal to the superfamily Fulgoroidea) are separated as the sister group of the Heteroptera + Coleorrhyncha + Cicadomorpha (Cicadoidea, Cercopoidea, and Cicadelloidea).

Within the Fulgoroidea there are from 16 to 21 families, three with only one or two genera. Each family will be listed and discussed after some general characters are mentioned. These families are divided into two or three clades, depending upon the author. The Delphacidae and Cixiidae both have a sword-shaped ovipositor. The rest do not. They are divided by the number of spines on the second hind tarsomere into two groups. One has a row of spines and includes the Meenoplidae and its sister group Kinnaridae, Derbidae, Achilidae, Achilixiidae, Dictyopharidae and its sister group Fulgoridae, and also the Cixiidae and Delphacidae. The nymphs of the first five families of this group and of the Cixiidae are thought to live underground or in association with the ground. The last group includes the Acanaloniidae, Caliscelidae, Issidae, Nogodinidae, Ricaniidae, Flatidae, Tropiduchidae, Tettigometridae, Lophopidae, Eurybrachidae, and the two small families Hypochthonellidae and Gengidae.

Habitats

Eight of the families are found on all the continents but Antarctica, and some are found in each major biome, including forests, grasslands, deserts, tropical rainforests, and arctic tundra. Three families are worldwide except for the Palearctic (fulgorids, nogodinids, acanaloniids), one except for the Nearctic (ricaniids), one except for the Holarctic (lophopids). The tettigometrids are not found in the New World or Australia. The Nearctic and Palearctic have 12 families each, Australia 15, the Neotropics 16 or 17, and Africa (lacking kinnarids and achilixiids) and the Orient (lacking gengids and hypochthonellids) each 19.

Most adults feed on plant parts above ground. Nymphs of cixiids are found in cavities underground, feeding on plant roots, often grasses. Nymphs of achilids and derbids have been found in cavities in rotten wood or under bark, where they are thought to feed on fungi. Kinnarid and meenoplid nymphs are supposed to be associated with soil, as are the three smallest families, achilixiids, gengids, and hypochthonellids. The other families, as far as reported, have the nymphs on the leaves and trunks of the same hosts as the adults.

Eggs are placed in several substrates. In delphacids and cixiids, they are inserted into the soil or plant tissue with a sword-shaped ovipositor. Derbids, achilids, kinnarids and meenoplids are thought to have a raking-sweeping type of oviposition, where the substrate is moved and the eggs are attached to small particles such as bark. Fulgoroids, dictyopharids, and eurybrachids are thought to glue eggs to plant surfaces, and the rest have a secondarily derived piercing excavating ovipositor. Most cover their eggs with wax. Two genera of issids (two in Europe, and one in California) carry dry soil in an internal sac and mix it with body fluids to form mud egg cases.

Adults of four families, cixiids, meenoplids, kinnarids, and delphacids, have been found adapted to caves, with eyes reduced or absent, wings often reduced, and loss of pigment, and adults of hypochthonellids burrow through the soil. Cavernicolous species have been found in caves or lava tubes chiefly in Australia and Hawaii, but also in Thailand, Mexico, New Caledonia, the Canary Islands, Galapagos Islands, and Western Samoa.

Fulgoroidea are one of the groups that have been successful reaching and establishing themselves on islands. Delphacids are the most successful and widespread, and obviously traveled as aerial flotsam, as they have been found in samples taken in nets on the prows of ships in the Pacific. Often they have maintained their specific identity, which may indicate repeated gene flow to the islands. In other cases, such as Hawaii, they have speciated successfully. Actually, 13 families have reached oceanic islands, including all of the families with nymphs associated with the soil (except hypochthonellids and gengids with their three species total), suggesting that rafting may be involved in some cases.

Hosts

Fulgoroidea, as far as is known, feed on phloem of plants, through roots, trunks or leaves, except for the Achilidae and Derbidae, which are thought to feed on fungus, at least as nymphs. In a few cases this has been demonstrated in various families of the order through histological studies of plant parts, tracing the stylet sheath secreted by the insect through or between the cells to a cell or to the phloem or xylem tubes. In others it is accepted because of the production of honeydew. Some species are known to be monophagous, but a flatid, *Metcalfa pruinosa* (Say), has been reported from 100 plants in the United States, and now has been accidentally introduced into Italy, where it has been found to be a pest of grapes especially, either the wax from the insect or sooty mold from the honey dew detracting from the appearance of the fruit. Monocots are popular hosts, especially rice, sugarcane, corn, and palms. Wilson et al. (1994) list the hosts for as many species as they could find references, finding ten families feeding on Pteridophyta, sevenon Gymnospermae, all but two of the 16 common families (Eurybrachidae and Nogodinidae) on Monocotyledoneae, and all on Dicotyledoneae. They also give fossil history and differing phylogenies of the group to consider the evolution of host plant use.

Pest Species

Fulgoroidea are implicated in rice diseases in the orient, lethal yellowing of palms in the Caribbean and Florida, and Dubas-bug-caused death of date palms in the middle east. An unusual pest is the ricaniid *Scolypopa australis* Walker from Australia, which, although it has many hosts, sometimes feeds on a poisonous plant tutu, *Coriaria arborea* Lindsay, producing a poisonous honeydew. In times of poor nectar supply, honey bees feed on the honeydew and produce a honey poisonous to man. A list of species reported as pests of crops is reported in Wilson and O' Brien (1987).

Communication

Although the cicadas communicate by airborne sounds, the Fulgoromorpha and the rest of the Cicadomorpha communicate by substrate-transmitted sounds scarcely or not audible to the human ear. Males and females in the families studied (cixiids, delphacids, dictyopharids) each have species specific mating sounds, with the males usually initiating the sounds and the females responding. Although the male genitalia are very complex and almost always species specific, the calls are considered significant in mating isolation as well as mate finding. Fulgoroids are not thought to produce pheromones.

Wax Production

Wax (actually a 60–80 carbon atom ester of 30–40 carbon acids and alcohols) is produced in most nymphs and females and some males in most members of the superfamily (rare in delphacids, only the vision of *Saccharosydne sacchivora* (Westwood) with waxy tufts comes to mind). Chemically it shares compounds found in the wooly alder aphid and the cochineal scale. Most of the wax is produced through hundreds of flower-shaped glands in wax plates on the sixth, seventh, and eighth abdominal tergites. Hollow strands are produced which touch each other to form another hollow tube. Small clumps of gland cells are usually found around the spiracles also. Wax particles as opposed to strands may also simply be excreted through the integument almost anywhere on the body, including the wings in some species, without an external gland visible by means of scanning electron microscopy.

What is the function of wax? Females cover the eggs with it and reports show the wax hides the eggs, repels water running over eggs, and may protect the eggs and nymphs from parasites. It is also thought to keep the nymphs in enclosed places from becoming sticky with their own honeydew, to aid escape from spider webs, to reflect ultraviolet light to aid species recognition (insects see in the ultraviolet), etc. Fulgoroidea feed on sugary phloem which they need to ingest in excess to get N for growth, and they need to get rid of sugars because of their osmotic effect on the hemolymph, but they don't have filter chambers. Might they simply have produced more of these high molecular weight compounds, some of which are similar in wax and in cuticular wax, to get rid of the excess sugar, and retained them for both physical and physiological benefits?

Other Behavior

The genera *Megamelus* (Delphacidae) and *Taosa* (Dictyopharidae) are able to live on emergent aquatic plants without all of the jumping nymphs drowning. Some of the fulgorids have favorite trees in the jungle and may be found on them for weeks at a time and year after year. A tribe of derbids can roll its wings longitudinally, presumably for protection from tropical rain drops. Tettigometrids, in a commensal arrangement with ants, can increase the production of figs. Poison honeydew from a ricaniid can be incorporated into honey, making it poisonous to humans.

Predators and Parasites

Four families of insects are parasitoids of planthoppers and leafhoppers, the Pipunculidae (Diptera), Dryinidae (Hymenoptera), Halictophagidae (Strepsiptera), and Epipyropidae (Lepidoptera), the latter inserting their mandibles through the intersegmental membranes and feeding on the hemolymph of several families of Fulgoroidea in the Nearctic, Neotropics, and Asia. Egg parasites include the Hymenoptera Mymaridae, Trichogrammatidae, Eulophidae, and Aphelinidae. Nematodes may also be parasitoids of nymphs and adults.

Birds are important predators. Up to 71% of the insects in stomachs of flycatchers have been found to be fulgoroids. It is assumed that other insectivores also eat them, although perhaps not preferentially. Man, from fear, is a killer of one genus in Brazil (see Fulgoridae, below).

Family Synopsis

Each family will be discussed alphabetically (refer to the listing above for phylogenetic sequence). If there is a single character that can separate that family from other Fulgoroidea, it will be mentioned. Otherwise, consult O' Brien and Wilson (1985) for a key, illustrations of morphology, and a general introduction to the superfamily.

Acanaloniidae

This mostly New World family can usually be recognized by the lateral flattening, reticulate venation, and green color in specimens of small to medium size, 4–12 mm. long. It was placed in the issids by Fennah (1954) but resurrected by Emelyanov (1999).

Achilidae

This worldwide family can be identified by the tips of the forewings overlapping at rest except in a few genera. A key to genera of the world is provided by Fennah in 1950. One species in Australia is found in termite nests. At present there is a disproportionate number of genera with few species in them in this family.

Achilixiidae

This small family of two genera and 24 species is found in the Neotropics and the Philippines and Borneo. They may be identified by a lateral projection of the abdomen topped by cup-like depressions. They are from 4 to 8 mm long. Bennini in the Cixiidae have a similar projection, but the top surface varies, and the cixiids have a branched spine in each depression. Achilixiids have been placed in the achilids, derbids, cixiids, and kinnarids. The function of the projection is unknown.

Caliscelidae

This worldwide group is found on bunch grasses in South America, grasses and sedges in the U.S., and also palms and bamboo elsewhere. It was only recently raised to family level (removed from the Issidae). They are small (3–6 mm long) and brachypterous, and are often taken for weevils or Heteroptera nymphs. Some are associated with ants.

Cixiidae

Female cixiids can be identified by a sword-shaped ovipositor and no moveable tarsal spur (delphacids also have the sword-shaped ovipositor). Males need a composite of characters. They are small or medium sized, from 3 to 13 mm long. Of worldwide distribution, they are probably the second most economically important group of Fulgoroidea because they transmit lethal yellowing of palms and other phytoplasmas.

Some have become of interest recently because they have adapted from epigean adults with nymphs feeding on roots underground to fully cave adapted species, with loss of eyes and pigment. This is particularly interesting in Hawaii, where some Oliarus have invaded lava tubes, which we have begun to date. Evidence from their recorded mating calls shows that cave species on Mauna Loa and Mauna Kea are more closely related to the epigean species above ground above them than the troglobitic (cavernicolous) species of the other mountain, even though there are fissures in the lava which would allow them to travel great distances underground.

Delphacidae

The delphacids can be recognized by the movable spur on the hind tibia. When sorting collections by eye, these specimens, 1–6 mm long, may usually be picked out of Auchenorrhyncha by their antennae sticking out from the side of their head, more visibly than other families. Economically, they are the most important of the Fulgoroidea. The Delphacidae include at least 55 species that feed on economic plants, including some major pests of agricultural crops, such as rice, sugarcane, maize, taro, and cereals. Plant damage results both from direct feeding, and the transmission of plant diseases, particularly viral diseases (e.g., Fiji disease of sugarcane by *Perkinsiella saccharicida*, rice grassy stunt and rice ragged stunt by *Nilaparvata* spp. (*Nilaparvata lugens*, a rice pest, cost China an estimated US $400 million loss in 1990), rice hoja blanca by *Tagosodes* spp., rice yellows by *Sogatella furcifera*, cereal mosaic and oat rosette virus by *Laodelpax striatella*, maize mosaic and maize stripe viruses by *Peregrinus maidus*). Note that the above list of delphacid-vectored plant diseases includes five of the top ten major world food crops (wheat, rice, corn, barley, and sugarcane), plus, at least three delphacid species are known to feed on sorghum.

Delphacids are carried easily by air currents. Rice pests reinvade Japan each year from China, and delphacids have probably reached every island in the world, but sometimes do not form new species on islands, presumably because other introductions of the same species do not allow reproductive isolation. They, and cixiids, seem most tolerant of cold habitats.

Derbidae

The derbids have a number of characteristic shapes, varying in size from 4 to 16 mm. It may be the possibility of tropical raindrops plastering their wings to a substrate with subsequent death that has favored the selection of multiple resting positions. Many have roof-like wings and sit head-up on plants, often grasses. Others, Mysidiini, are moth-like and hold their wings flat against the underside of broad leaves. Specimens of Zoraidini hang upside down, frequently on palm leaves, with the wings held together under the back, forming a T-shape with the body in lateral view. Specimens of Dawnarioidini have the ability to roll each pair of wings into a longitudinal tube, which is held above the body and to the side, forming a V shape in caudal view. Specimens tend to congregate on the same leaf or on the same plant.

Dictyopharidae

The dictyopharids, sister group of the fulgorids, are often green and with a head projection, but do need to be keyed to family. They vary in length from 3 to 33 mm. One genus, *Taosa*, lives on aquatic plants and a species is being tested to see whether it is host specific and may be used for biological control of water hyacinth. The nymphs seem to be able to fall onto the water and get out again, perhaps because of broad spines on the hind tibiae and tarsi. A desert loving subfamily, Orgerinae, is small and brachypterous and lacks the tegulae found in the rest of the Fulgoroidea.

Eurybrachidae

Found in Africa, the Orient, and Australia, these insects usually can be identified by the rectangularly (not triangularly) shaped wings, the frons being 3× as broad as long, and the second hind tarsomere lacking spines. Usually the forewings are opaque and colored. They measure 8–28 mm in length. In Australia they are associated with *Eucalyptus* and *Acacia*. In both an Asian and African genus, the forewings are modified with a projection that looks like an antenna, and the hind wings with one that bends downward like a snout, so the insect appears to have two heads, but the false one is the more obvious.

Flatidae

This family has the second most colorful and second largest specimens (4.5–32 mm) of the superfamily after Fulgoridae. They can be identified by having pustules in the basal half of the clavus plus the costal area transversed by many parallel veinlets. Many species (46%) are polyphagous, so introduced species may become pests, as *Metcalfa pruinosa* (Say) has in Italy and Southern Europe, introduced from the U.S.; *Siphanta acuta* (Walker) may become a pest in Hawaii and California, introduced from Australia or New Zealand; and *Melormenis basalis* (Walker) may in Florida, introduced from the West Indies.

Fulgoridae

This family, known for large (up to 10 cm) and colorful specimens, is also known for large and colorful legends. It can be identified by cross veins in the hind wings. The largest number of genera and greatest variation in the head shape are in the Neotropics, but the greatest variation in color occurs in Asia. This family does not reach the Palearctic. The nominate genus, *Fulgora*, was called a lantern fly because of its large peanut shaped head that suggested a lantern and was reported to produce light, with the last report in 1951. Now it is accepted that it does not bioluminesce, but the natives in the South American jungle still fear it, saying it kills anything it touches, perhaps because the head looks like an alligator in lateral view, with a false eye spot, a false nostril on the top of its head and a row of false teeth. Presumably this mimicry works on birds and perhaps monkeys, and perhaps man in the past, when the medicine man carried a dead Fulgora in his amulet bag. But a Brazilian ethnoentomologist, Eraldo Medeiros Costa Neto, says now people get a big stick and try to kill the insects. Male college students, on the other hand, from Mexico to Argentina, have asked if they will die if bitten by a Fulgora if not saved by having sex within 24 h.

Gengidae

This family of two genera and two species is found in the Union of South Africa. Their nearest relative is thought to be Eurybrachidae.

Hypochthonellidae

This family is known from adults and nymphs of one species taken underground on the roots of corn, tobacco, and peanuts in Southern Zimbabwe. The compound eyes are obsolescent, the ocelli absent. The wings are brachypterous and the adult described as maggot-like. It most seems to resemble Flatidae.

Issidae

This large family of small to medium insects, 2–19 mm long, are often brown and a rounded diamond shape from above. There is still a question whether the family is monophyletic. Females of one genus, *Hysteropterum*, which occurs in Europe and the U.S. (and a second genus in Europe), scratch up dirt and store it in a sac near the ovipositor and use it with bodily secretions to make a mud case for the eggs.

Kinnaridae

Kinnaridae and Meenoplidae are sister groups, identified by wax on the females on their chevron-shaped sixth to eighth tergites, or the wax plates, if the wax is lacking. Both are thought to have nymphs that live underground or near the ground. Kinnarids are found primarily in the New World, and are especially common in the West Indies. They are from 2 to 8 mm in length.

Lophopidae

The Lophopidae, found everywhere but in North America and Europe, with one genus (*Carrionia*) in South America, are the first family to have a complete modern cladistic treatment at the generic level. *Pyrilla perpusilla* (Walker) can be a pest of sugarcane, rice, and corn in India. Lophopids vary in shape and color and in length from 6 to 15 mm. A fossil has been found in North America, although no species are present there now.

Meenoplidae

The meenoplids, a small family of small insects, 3–7 mm, can be recognized by the combination of chevron shaped wax-bearing 6–8 tergites in the females and pustules on one or both claval veins. Kinnarids, their sister group, have the same shape of the wax glands, but lack the pustules on the forewing. Meenoplids are not found in the New World and are associated with the soil in the literature. Cave dwelling species are found in Australia, New Caledonia, the Canary Islands and Western Samoa.

Nogodinidae

Tribes in the nogodinids, lacking in the Palearctic, are still being moved from family to family in the hope of delineating a monophyletic group. Wings are usually broadly oval, usually membranous or with a membranous cell. They vary in size from 4 to 17 mm. Fennah moved some of the issids in California to nogodinids and acanaloniids to issids; Emelyanov (1999) moved both Caliscelinae and Acanaloninae back to families, and moved Bladininae to Issidae, based primarily on the structure of the ovipositor.

Ricaniidae

Sub-triangular fore wings separate most species of this family from the rest of the Fulgoroidea. They are found everywhere but in the Nearctic, range from 6 to 20 mm, and are usually membranous with dark patterns or dark with membranous areas. *Scolypopa australis* can cause honey poisoning.

Tettigometridae

Tettigometrids lack some of the characters usually found in Fulgoroidea. They have been considered the most primitive, but now are considered among the more recent families. They are not found in the New World or Australia, are 3–7 mm long, with the wings shaped to the body, and lack a jumping apparatus. They are often associated with ants which remove their honeydew and protect them in return. In tropical Africa Camponotus ants which feed on the honeydew of *Hilda undata* (Walker) can reduce the predation on pollinators and figs by other species of ants.

Tropiduchidae

Tropiduchids are found worldwide and can be identified in most species by a transverse groove between the apex and disk of the mesonotum. They are usually green, depressed, and similar to dictyopharids but have only one pair of spines on the hind tarsomere and the venation is different with fewer apical cells. Sizes range from 5 to 13 mm. *Ommatissus lybicus*, the Dubas bug, can kill date trees in the Middle East.

Current Status

In no country of the world can one identify all of the species of one family of Fulgoromorpha with a single reference except England, Scandinavia, New Zealand, and perhaps Taiwan. But new species are still being discovered in Taiwan. Europeans say they can identify the species of Middle Europe, but Spain and Portugal, southern Italy, and Greece and Turkey are poorly known. Also, the U.S. and Canadian faunas are known and most species can be identified, with the western flatids and delphacids being the most troublesome. There are many papers on the fauna of national parks in Africa, but nothing I know of that relates the Entomofaunal regions to these papers. European museums have many species from the Orient, so perhaps some sort of monograph might be done, but surely many species have not been discovered. Australia has many species to be described. South America is virtually unknown. Judging from 852 described species in the U.S. and Canada and 750 in Taiwan, their museums are obviously incomplete.

Further Information

The Metcalf catalog is superb, with notes on whether each paper cited contains information on keys, description, illustrations, biology, host, etc. Unfortunately, it is out of date, as is the bibliography that accompanies it.

Review papers which provide an introduction to the superfamily (O' Brien and Wilson 1985), to pest species (Wilson and O' Brien), to behavior (O' Brien 2002), to host preferences (Wilson et al.) are listed below. The book "The Planthoppers and Leafhoppers" (Nault and Rodriguez, eds 1985) and a volume of Denisia (2002) provide a series of papers of related review articles.

Fennah (1950) keyed the achilid genera of the world. Fennah also has provided keys to Neotropical genera in derbids, dictyopharids, kinnarids, and tropiduchids, and in the "Fulgoroidea of Fiji" a key to Australasian cixiids, delphacids, derbids, and Pacific issids, tropiduchids and ricaniids. Earlier treatments of the world fauna, or a large part, such as Melichar's (1898–1915) can be located in Metcalf's catalogue. A recent paper (1998) keyed the genera of Lophopidae, and subsequent ones, also by Soulier-Perkins (2000, 2001), describe their phylogeny and biogeography. Denno and his students have done many ecological studies to provide a theoretical background for pest management practices, emphasizing studies on the effect of brachyptery in a dimorphic species.

Bourgoin, Campbell, Asche, and Emelyanov are doing phylogenetic studies between and within families. Porion (1994) and Nagai and Porion (1996) have provided photographic atlases and checklists of the Fulgoridae of America, and of Asia and Australia, with many colored plates.

► Bugs (Hemiptera)

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Plant Lice

Members of the family Aphididae (order Hemiptera).

► Bugs
► Aphids

Plant Resistance to Insects

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Plant resistance to insects is a natural phenomenon based on plant self-defense mechanisms. It results from insect-plant co-evolution and is crucial for their co-existence. During plant domestication, some important features of plant resistance may be inadvertantly removed by the breeders, increasing their susceptibility. This necessitates additional selection for resistance factors.

When plant breeding was still performed under field conditions, the most susceptible plants were so badly damaged by insects that they were lost from the breeding pool before they produced seeds. Thus, the plant population retained a natural resistance to insects. After World War II, however, massive use of insecticides by plant breeders accelerated the loss of natural resistance in crop plants, because it allowed the conservation of plants that were high yielding but, on the other hand, very sensitive to insects. As a result, these modern, high valuable cultivars must be continuously protected against pests. The solution to this problem lies in an attempt to reincorporate resistance into the modern crop varieties. This task requires a clear definition of the breeding target(s), adequate source(s) of resistance, and development of methods to evaluate resistance that are reliable, inexpensive and rapid. Plants and insects are very dynamic, and highly developed organisms with a good capacity for adaptation to ever-changing environments. Because insects are capable of evolving, and overcoming plant resistance, a suggested strategy is to implement an Integrated Pest Management (IPM) program that combines partial plant resistance with nontoxic (e.g., biological, physical, biorational) control measures.

The Nature of Insect Damage to Plants: Direct Versus Indirect Damage

There are two main types of insect damage to plants: (i) Direct damage is caused by insect feeding on the plant resources. This may be accompanied by insect excretion of honeydew, on which a black sooty mold develops. The damage is correlated with pest population size. (ii) Indirect damage is caused by the insect transmission of plant diseases (viruses, mycoplasma, etc.), and can be caused by a rather low vector population. Accordingly, the crop resistance breeding program should include two different breeding concepts: (i) Prevention of direct (quantitative) damage will be achieved by suppressing pest population buildup, to keep it below the "Economic Injury Level" (EIL). (ii) Indirect damage can be prevented by breeding for "vector resistance," minimizing virus transmission by insect vectors.

Definitions of Plant Resistance to Pests

Plant resistance is defined as any reduction in plant acceptance, in pest population growth rate, or in the damage cause by pests, that is due to inherited self-defense mechanisms in the plant. If the EIL is not reached until the end of the crop production season, the plants are considered resistant (R) to that specific pest. If the EIL is exceeded during the crop production season, the plants are considered partially resistant (PR). If the EIL is reached even before the crop production has started, the plants are designated as susceptible (S). Immune plants are plants which are not attacked at all, whereas tolerant plants are plants which possess a high EIL.

Mechanisms of Resistance

The mechanisms of resistance can be divided into two major categories: antixenosis and antibiosis, which often occur together. Antixenosis is related to arthropod behavior that leads away from plant damage, whereas antibiosis is related to poor performance or lethal effects on different stages of the target insect. Although complete resistance to insects has been found and used, it is rather exceptional. On the other hand, the more frequently occurring partial resistance tends to be more durable, which is an important advantage for the development of stable agro-ecosystems. Introducing partial resistance requires more sophisticated testing methods.

Plant resistance to insect pests based on recombinant proteinase inhibitors (PIs) could interfere with natural enemies of target pests, as their own proteolytic systems may also be sensitive to broad-spectrum proteinase inhibitors.

Vector Resistance

Resistance to vectors is a special case of plant resistance to pests. Vector resistance is the tendency of plants, which are by themselves virus-susceptible, to escape infection by preventing the vector from transmitting the virus. Hypothetically, two mechanisms of plant resistance are recognized: resistance or tolerance to the virus itself, and resistance to the vector which transmits the virus.

Various insects transmit virus diseases to plants. Most insect vectors belong to the Hemiptera (e.g., aphids, whiteflies, mealybugs, psyllids). All are phytophagous, piercing the plant with their mouthparts (stylets) to suck sap from the plant tissues. Viruses are transmitted in a rather short time of inoculation-feeding, usually within minutes when they are "stylet-borne" (non-persistent) viruses, or within few hours if they are "circulative" (semi-persistent or persistent) viruses. Stylet-born viruses are "mechanically transmitted" when the insect probes the plant, whereas circulative virus transmission requires vector feeding upon the plant.

The advantage of breeding resistance to the insect vector is twofold: it can be integrated with plant resistance, or tolerance, to the virus itself, and plant resistance to insects is expected to be of greater durability than plant resistance to viruses. Several plant features can be responsible for this kind of resistance: hairy leaves, sticky and poisonous secretions, and intrinsic factors in plants which influence the settling, acceptance, and feeding behavior of the insect vector (such as the secretion of an aphid alarm pheromone mimic by the plant).

Some projects have been based on the advantage of breeding vector resistance. A significant reduction of Tungro virus was achieved in rice by the use of cultivars resistant to the leafhopper vector, *Nephotetix impicticeps*. A similar result was obtained by using cultivars resistant to *Nilaoarvata lugens*, the vector of the grassy stunt virus in rice. Resistance to *Aphis gossypii* of *Cucumis melo* prevented the transmission of cucumber mosaic virus (CMV). *Solanum polyadenium*, *S. berthaultii* and *S. tarijense* reduced attacks by aphids, and thereby reduced the viruses they transmit to potatoes. Cassava cultivars, which are partially resistant to *B. tabaci*, significantly reduce the incidence of African cassava virus.

This type of resistance may have also some drawbacks because it is vector specific, but not virus specific. The resistance to CMV transmission in muskmelon, for example, appears to be associated with nonpreference for *Aphis gossypii*. Though this plant was completely resistant to the transmission of several strains of cucumber mosaic virus (CMV) by *A. gossypii*, it was susceptible to inoculation by *Myzus persicae*. Furthermore, once this cultivar became infected, it was a source of CMV for both *A. gossypii*, and *M. persicae*. This cultivar is also resistant to CMV transmission by several clones of *A. gossypii*, and to the transmission of some other viruses as watermelon virus 1 (WMV_1), WMV_2, and muskmelon yellow stunt virus (MYSV) by this vector. However, it was susceptible to the transmission of these viruses by several other aphid species. Conclusively, this type of resistance to transmission is vector specific, but not virus specific.

Methodology: Evaluating Plant-Resistance to Insects

Methods to evaluate levels of plant resistance to both the direct or and indirect types of damage are crucial for any breeding program of plant resistance. The method should be quick, cheap, and reliable.

One of the first steps to a deliberate exploitation of genetic variation in host-plant resistance would be large-scale screening of a wide collection of varieties, breeding materials, or related wild species. The search for resistance should not be limited to free-choice experiments since the differences found are obscured when varieties are grown in monoculture. Thus, at least the most promising materials should be tested by non-choice experiments as well, to make sure that the differences found are based on true resistance and not merely on preference (antixenosis). Results should be carefully interpreted and conclusions limited to the varieties used in the experiments. Laboratory studies must, likewise, be cautiously viewed because laboratory cultures of insects suffer greatly reduced genetic variability. The strain and origin of the insects used should also be specified.

Plant Resistance to Pests Causing Direct Damage

Direct damage is usually correlated with pest population densities. Hence, host preference, rates of feeding, and rates of the pest population built-up, like the "innate capacity of population increase" (r_m), provide powerful tools for choosing a suitable source of resistance and for determining the level of resistance among the progenies. A quick and reliable test of resistance, in plants in which a sticky exudate is the mechanism of resistance, is the "sugar-test." Fine-ground crystallized "tea" sugar is spread on the tested leaf, the excess of sugar is shaken off, and a leaf diskette of a determined area is punched out from the treated leaf. The sugar is washed off from the leaf diskette, and the amount of sugar in the aqueous solution is determined with a refractometer by means of a pre-prepared correlation graph.

An additional method to evaluate plant resistance is based on the expression of resistance in in-vitro derived callus tissue rather than in seedlings or complete plants.

Evaluation of Vector Resistance

Plant resistance to stylet-born viruses may be evaluated by confining viruliferous insects (insects contaminated with plant virus) onto test-plant seedlings. After the virus incubation time has passed, the percentage of plants showing virus symptoms is determined.

A much quicker technique is, once a correlation graph has been produced, to relate virus incidence to the amount of feeding or to the excretion rates. For example, the amount of excreted honeydew often directly reflects the probability of TYLCV transmission by *B. tabaci*. The rate of honeydew excretion can be quantified by counting the number of droplets, or by determining the amount of sugar in the excreted honeydew. The honeydew can be collected by confining the whitefly adults onto the underside of a healthy tomato leaflet by means of a clip-on-cage, or by a modified "Munger-cell." If a detached leaf is used, its petiole must be kept moistened to avoid leaf desiccation during the test. The honeydew can then be collected on a piece of filter-paper, and treated with a reagent (Ninhydrin 0.2%) that stains the amino acids of the honeydew blue. The droplets can then be easily counted. To determine the total sugars, the honeydew is collected on a microscope glass cover slide and washed off with 1 ml of distilled water, to which 2 ml of a 0.2% Anthrone solution had been added. The optical density of this solution is then recorded by a spectrophotometer at 620 nm. The absolute amount of sugars in the honeydew is then derived from a pre-prepared calibration curve. Such tests are performed within 4 or 24 h.

Sources of Resistance

Genetic sources of resistance to insects can be introgressed into modern crop cultivars. Many "old" or "primitive" varieties of crops that have been under cultivation for a long time, such as rice, eggplants, cucumbers, etc., can be investigated as sources for resistance. However, such "new world" crops as tomato, potato, pepper or corn, which have been under cultivation for a relatively short period of time, often lack known resistant cultivars, so resistance must be searched for and acquired from wild plants that can be interbred with these crops. Some examples are given below.

Soybeans

Leaf pubescence influences oviposition of *Bemisia* on soybean, *Glycine max*. More eggs are laid on hirsute and pubescent than on glabrous isoline. The within-plant distribution of eggs is related to trichome density.

Cotton

Glabrous cotton confers resistance to the *Heliothis* spp., but numbers of tarnished plant bugs and cotton flea-hoppers are greater on pilose lines; damage is reduced depending on the degree of pilosity. *High gossypol*, due to genetic increase of gossypol naturally occurring in cotton, causes the death of larvae through antibiosis and phagodeterrence. It was found to inhibit protease and amylase activity in *Spodoptera littoralis* larvae. High tannin causes antibiosis and feeding deterrence to *Heliothis* spp. *Nectariless* has been shown to be a resistance character for pink bollworm based on antibosis. (Transgenic cotton, to which the gene responsible to the development of the toxin of *Bacillus thuringiensis* has been transferred by genetic engineering manipulations).

Engineered Resistance

There is interest in more rapidly creating plant resistance to insects. An induced method for obtaining resistant mutants might be achieved by irradiation or by transgenic manipulations. Plant genetic engineering offers opportunities for the creation of insect-resistant plants by insertion and expression of entomopathogenic proteins.

Techniques for gene transfer have been developed for most crop plants, but current prospects for engineering resistance to insects are limited by our lack of identified candidate genes to transfer, our elementary stage of understanding of gene regulation in plants, and uncertainty about the acceptance of engineered organisms by society. Most plants genetically engineered for resistance to insects and currently being tested in the field derive their resistance from a protein endotoxin from one of the many strains of *Bt* (*Bacillus thuringiensis*), a bacterium long used as a microbial insecticide. Examples of this are transgenic cotton or potato plants to which the *Bt* toxin gene had been transferred, or transgenic clones of *Bt*-1 that impose resistance to the potato tuber moth. Some tomato varieties, bearing the Mi-1.2 gene, which provides resistance to nematodes (*Meloidogyne* spp.) and to the potato aphid (*Macrosiphum euphorbiae*), are also less preferred by *Bemisia tabaci* than varieties that do not bear this gene.

The potato proteinase inhibitor gene, pin2, was introduced into several rice varieties and inherited. Bioassay for insect resistance with the fifth-generation transgenic rice plants showed that transgenic rice plants had increased resistance to a major rice insect pest, pink stem borer (*Sesamia inferens*).

Environmental Factors Affecting Resistance

Environmental factors such as day-length, light intensity and plant nutrition, affect not only the development and behavior of the insects but also the morphology and physiology of the plant. Temperatures, drought, plant nutrition, plant age and previous virus-infection may also affect the hostplant preference of the insect, which is then expressed as variations in plant resistance by making a susceptible plant to appear "resistant." Furthermore, the conditions under which the resistance-test are performed must also be optimized, standardized and noted.

The Effect of Light Intensity and Photoperiod

Some *Lycopersicon pennellii* and *L. hirsutum* f. *glabratum* accessions are always resistant to *B. tabaci*, some are always susceptible, but in some accessions the resistance varies according growth conditions, summer or winter. Both light intensity and day-length (photoperiod) affect their resistance to *B. tabaci*, *Manduca sexta*, and to *Leptinotarsa decemlineata*. Furthermore, 2-tridecanone, a toxin important in the resistance of *L. hirsutum* f. *glabratum* accessions, is significantly more abundant in plants grown under long day than under short-day regime. Accessions of *L. hirsutum* f. *glabratum* varied in their resistance to *B. tabaci* when grown under low light intensity, independent of day-length. In the case of *L. pennellii* accessions, only plants grown under low light intensity and a short-day regime are susceptible. The density of glandular trichomes, which secrete 2-tridecanone, is influenced by an interaction between day length and light intensity. Hence, the transition from resistance to susceptibility and vice versa took about 3–4 weeks and found its expression in the leaves, which had grown under the new conditions. The resistance can be noted clearly by the stickiness of the leaves, as quantified by the "sugar test." Day length also has significant effects on the expression of resistance in *L. hirsutum* leaves to *L. decemlineata*, through the tomatine content of the leaves which affects the rate of feeding.

The Effect of Plant Nutrition

Concerning their effects on insects, plant biochemicals may be divided into nutrients and non-nutrients. The effect of nutrients on hostplant specificity is small. Variations in nutrient value of plants are usually not significant. Furthermore, most species of insects do not differ greatly in their qualitative requirements for nutrients. Thus, although the host plant obviously has to satisfy the nutritional requirements of the insect, it does not seem likely that the insects' nutritional requirements play more than a minor role in host plant specificity. Allelochemics (non-nutritional chemicals produced by an organism) which affect the growth, health, behavior, or population biology of insects, can be extremely important factors in host plant resistance. They may also interact with the nutrients.

In cultivated crops, artificial fertilization may have an important impact on insect-host-plant relations. In many crops, nitrogen fertilizer increases the number of pests because they affect the suitability of the plant. But in some pest-crop systems, the same nitrogen levels may have a negative impact on plant resistance; this can occur in forests and, less often, in grass, where nitrogen decreases pest numbers for reasons which are unclear. Generally, pest populations increase when the host plants are over-fertilized, especially when nitrogen is in excess. High N-levels in the hostplant cause an increase in aphid populations. In whitefly, increasing N-levels in the plant nutrition causes an increase in the intrinsic rate of natural population growth (r_m) due to an increase in survival, fecundity, respiration rate, net reproductive rate (R_0), followed be an decrease of generation time and in the doubling time of the populations.

Increasing population growth enhances not only direct damage but also the development of resistance to pesticides, which will undoubtedly result in positive feedback by a significant, and completely unwanted, increase in pesticide application.

The effects of P and K, as well as minor and trace elements, are less clear. The idea that K is outstandingly important in conferring "resistance" to pest attack has found little support. Undoubtedly, the composition of cell sap is affected by the nutrients applied to soil as N, P and K, and may sometimes enhance or reduce the real resistance of the crop to particular pests by modifying non-preference or antibiosis. The effects might well operate in different directions for a variety of pests attacking the same crop.

Glucosinolates and the availability of free amino acids in the phloem affects the feeding behavior and development of the specialist cabbage aphid, *Brevicoryne brassicae*, and of the generalist peach potato aphid, *Myzus persicae*, on *Brassica* species and cultivated cabbage.

► Allellochemicals
► Plant Secondary Compounds
► Trichomes and Insects

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Plant Secondary Compounds and Phytophagous Insects

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Although phytophagy is limited to eight (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, Phasmatodea and Thysanoptera) of the approximately thirty orders of insects, the diversity of herbivorous insect species is extensive. While the total number of phytophagous insect species is difficult to assess because of the overwhelming diversity of insects as a group and the large number of non-described species, it has been estimated that approximately 46% (or 361,000) of the almost 800,000 species of insects are herbivorous. Because plants and animals differ substantially in their chemical makeup (plants are composed primarily of C-based carbohydrates, while the primary biological macromolecules of animals are N-based proteins), strictly phytophagous animals face two major hurdles during feeding. First, nitrogen accounts for approximately 7–14% of the dry mass of animal cells, while plants rarely exceed 7% and are typically much lower. As a result, plants are nutritionally sub-optimal and N often is limiting for herbivores. Numerous studies have documented the direct positive relationship between N fertilization of host plants and increased size, fecundity and population density of plant-feeding insects.

Second, plants may employ either physical defenses such as thorns or trichomes, chemical defenses, or both for protection from attack by phytophages. Secondary compounds are substances that have no known metabolic function (i.e., they are not constituents of any known primary metabolic pathway). Moreover, secondary compounds are often energetically expensive to produce and, although a defensive role of plant chemicals was proposed more than 100 years ago, it wasn't until Fraenkel in the 1950–1960s specifically noted that host-location and feeding behavior of herbivores is regulated by plant secondary compounds. Secondary metabolites can be classified according to their concentration within plant tissues. Generally, plants or plant parts that are low in abundance (i.e., non-apparent to herbivores) produce qualitative defensive compounds that interfere with metabolic pathways of herbivores; whereas, common (i.e., apparent) plants or plant parts are more likely to be defended by quantitative compounds, which are produced in much higher concentrations and reduce the digestibility of the plant material. The concept of strategic chemical defense of plants, based on the visibility of the plant to searching herbivores, is referred to as the "plant apparency hypothesis" of chemical defense.

Secondary compounds can be broadly classified into two groups: N-containing and non-N-containing (Table 13). Among the N-containing compounds, non-protein amino acids, which are commonly found in the seeds of legumes, act as anti-metabolites because they are structurally similar to one of the twenty amino acids required for normal protein synthesis. For example, azetidine 2-carboxylic acid is structurally very similar to the protein amino acid proline and, as a result, it is mistakenly incorporated into the structural and enzymatic proteins of herbivores that consume the seeds. Incorporation of these toxic non-protein amino acids by non-adapted herbivores is likely to be fatal. However, some specialist seed-eating bruchid beetles have evolved the ability to overcome these toxic amino acids. For instance, larvae of *Caryedes brasiliensis* feed exclusively on seeds of the tropical legume *Dioclea megacarpa*, which contains high levels of the non-protein amino acid canavanine. Canavanine is similar structurally to the protein amino acid arginine. However, this bruchid beetle has very specific arginyl t-RNA synthetase, which discriminates between arginine and canavanine so that the latter is not incorporated into the insect's proteins. Glucosinolates, characteristic of the mustard family (Brassicaceae), are another important group of N-containing secondary compounds that also possess sulfur. While the glucosinolates vary in their side chains, they all contain thioglucose and sulfate moieties. Plants such as mustard and horseradish that synthesize glucosinolates also produce thioglucosidase, which enzymatically hydrolyzes glucosinolates by cleaving glucose and HSO_{4^-} from the parent molecule to produce isothiocyanate, thiocyanate or nitrile. Although glucosinolates are isolated from the thioglucosidase within the intact plant tissues, disruption of the plant structure by chewing or grinding action will cause glucosinolates to mix with the thioglucosidases resulting in hydrolysis and release of mustard oils. These pungent compounds (mustard oils) can cause blistering, irritation of mucous membranes including the alimentary canal, and they result in rejection of plant tissue containing them by non-adapted insects. For

Plant Secondary Compounds and Phytophagous Insects, Table 13 Select classes of secondary compounds produced by plants and their major effects on non-adapted insect herbivores (see text for details)

Classification	Class	Example	Common source	Effects on non-adapted insects
N-containing				
	Non-protein amino acids	Canavanine	Legume seeds	Antimetabolite, malfunctioning proteins
	Glucosinolates	Sinigrin	Mustard family	Anti-feedant, blistering, irritation of mucus membranes
Non-N-containing				
	Rotenoids	Rotenone	Legume	Inhibition of cellular respiration
			Roots	
	Pyrethrins	Pyrethrin I	Flower heads of *Chrysanthemum cinearifolium*	Paralysis
	Proanthocyanidins	Procyanidin	Most classes of woody plants, such as oaks	Precipitation of plant and insect proteins, reduction in insect size, performance and fecundity

instance, a concentration of ≥0.1% sinigrin (a glucosinolate) infiltrated into celery leaves was fatal to the non-adapted black swallowtail (*Papilio polyxenes*). Moreover, plant concentrations of as little as 0.01% sinigrin increased the development time of larva to pupa by 21%, reduced pupal mass by approximately 28%, and adult females laid 31% fewer eggs compared to insects reared on control plants containing no sinigrin. In addition, females, which had been reared as larvae on 0.01% sinigrin, only produced half as many viable eggs as females that had been cultured on plants containing no sinigrin. However, specialist herbivores such as the cabbage butterfly (*Pieris brassicae*), which feed exclusively on mustards, may utilize the pungent glucosinolates or their hydrolytic products for host location and to stimulate gustation. The cabbage butterfly may even reject artificial diet unless it contains glucosinolates or mustard oils.

The non-N-containing secondary compounds include some economically important substances such as the rotenoids and pyrethrins, which are used commercially to control insect pests of crops and turf grasses. The rotenoids (such as rotenone), primarily isolated from the roots of tropical legumes, prevent cellular oxygen uptake in insects by inhibiting NADH-dependent dehydrogenase activity associated with the electron transport system of mitochondria. Rotenoids are highly toxic to insects and as little as 0.003 g/g body mass was lethal to the silkworm (*Bombyx mori*). Pyrethrins, which may disrupt the permeability of nerve cell membranes to sodium ions, causes paralysis and death of insects.

Among the most widespread of the quantitative defensive compounds are the non-N-containing tannins. These C-based defensive compounds can be divided into two categories: hydrolyzable, which are derivatives of phenolic acids and condensed (proanthocyanidins), which are often of higher molecular mass. The name “tannin” refers to the ability of these substances to render animal hides into leather, which are much more resistant to water infiltration. Their ability to “tan” leather is based on the formation of hydrogen bond cross-links between tannin and protein molecules. The protein binding ability of tannins also provides protection to the plant from herbivores. Defensive tannins typically are stored in vacuoles, which prevents them from interacting with the plant's proteins. Upon disruption of the vacuoles, which occurs during herbivore feeding activities, tannins are released from the ruptured vacuoles and they quickly combine with available proteins. As a result, tannins greatly decrease the quality of the plant tissue by combining with two important groups of proteins. First, they combine with plant protein, which reduces the ability of proteases such as trypsin to digest them into simpler polypeptides for N metabolism in the herbivore. Second, they bind to the digestive enzymes of the phytophage, thereby reducing their ability to breakdown plant proteins (and other enzymatically digested compounds). This non-selective cross-linkage of proteins (both host's and herbivore's) can reduce the N availability (and hence quality) of the plant. The negative relationship between tannin levels and insect herbivore abundance was most clearly demonstrated by Feeny (1970) for the winter moth, *Operophtera brumata*, which feeds on leaves of the oak *Quercus robur*. Larvae of the winter moth feed on oak leaves during the spring, but quickly cease feeding on the oaks by mid-June when they search for alternative hosts. This sudden decrease in feeding activity is inversely correlated with levels of leaf tannin, which are low during the spring and rapidly increase during the summer. In laboratory studies, larvae of the winter moth reared on oak leaves collected on May 16 (prior to tannin buildup) were approximately 2.5 times heavier (peak mass) than larvae reared on leaves collected on May 29 (when tannin accumulation had reached approximately 1% of the dry leaf mass). The decrease in larval mass is important biologically because numerous studies have documented the correlation between larval or pupal mass and insect fecundity.

In summary, most vascular plants probably contain one or more secondary compounds. Although a defensive role has been hypothesized for secondary compounds, it is unclear whether this description is suitable in all cases. For instance, tannins (along with lignins) also help strengthen plant structures and prevent invasion by pathogens, in addition to their anti-herbivore role. Moreover, secondary compounds, while protecting the plant from attack by non-adapted herbivores, may actually serve as host selection cues and feeding stimulants for adapted insects. Although many of these substances such as tannins have general anti-herbivore properties and offer the plant protection from most herbivores, others such as such as pyrethrins offer protection from insect phytophages in particular.

► Allellochemicals

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Plant Viruses and Insects

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The principal families of insect vectors which cause the most damage to agricultural crops through the spread of plant diseases are in the order Hemiptera, and include the aphids, leafhoppers, delphacid planthoppers and whiteflies. Another important group of insect vectors found worldwide is the order Thysanoptera, the thrips. Other insects also spread plant diseases; however, aphids alone are responsible for spreading the majority of known plant viral diseases, followed closely by the leafhoppers, whiteflies, and thrips. The known number of plant disease vectors within these taxa is large, including Cicadellidae (leafhoppers, containing 49 known vector species), Aphididae (aphids, with the majority of 192 vector species), Aleyrodidae (whiteflies, with three vector species) and Thripidae (thrips, with eight known vector species). Of course, these numbers change every year with the description and discovery of new viral diseases and new insect vectors. Furthermore, a group with only a few insect vectors still may be able to carry and spread a huge number of viral diseases to many different host plants, as occurs in the whiteflies and thrips.

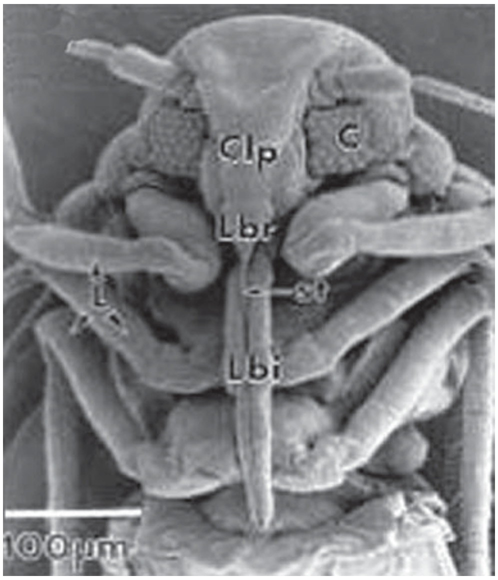
In 1997, more than 380 viruses were known to be transmitted by these insect vectors; however, in the last 5 years the number has increased greatly (about 600 in 2001) and is increasing every year. This dramatic increase has been due in part to our ability to detect and characterize viral diseases more accurately, and also due to increased travel and trade between countries, which often result in the accidental introduction of either diseases or insects from one country into another.

Components Involved in Disease Epidemiology

The epidemiology of plant diseases caused by insect-carried plant pathogens involves four main components: the pathogen, the insects, the plant and the environment. Thus, the transmission of a plant pathogen by an insect to a plant appears relatively simple. However, this situation is highly complex when one examines all the possible elements that can influence these interactions. The availability of the pathogen is affected by its quantity, location, and the strain within the plant. The insect's biology is influenced by population size, number of generations, longevity, dispersal patterns, feeding behavior and interactions with the pathogen. The plant's performance can be influenced by its level of susceptibility to the pathogen, multiple infections of different strains, and/or different pathogens, susceptibility to the insect, the location and stage of growth when exposed to the pathogen and insect. Environmental factors add another level of complexity as temperature, moisture, air currents, and cultural practices come into play. The discovery of a new plant pathogen that is carried and spread by an insect is usually the beginning of a long and difficult task toward understanding its epidemiology (all the elements that influence the development and spread of a plant disease).

Insect Feeding Mechanisms

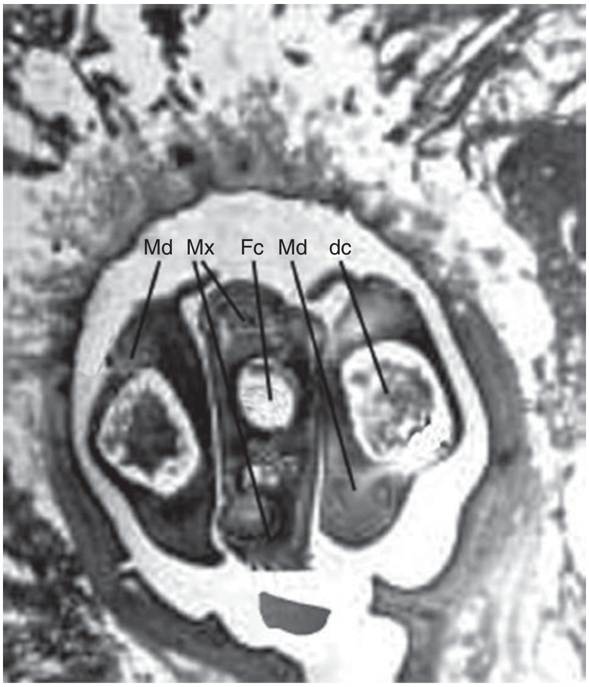
The traits of morphology that contributes to the ability of these insects to transmit plant diseases so efficiently is their piercing-sucking feeding style. Insects in the order Hemiptera (aphids, leafhoppers, whiteflies), and Thysanoptera (thrips) have similar basic morphologies of the head and body (Fig. 72–74). In the accompanying scanning electron micrograph you can see the compound eyes, and the proboscis of the insect. In Thrips this proboscis is referred to as a mouthcone due to the thick, short nature of the structure. The proboscis helps support the stylets as the insect works its stylets into the plant cells. The stylets are under muscular control so that they can be extended into the plant tissues. The stylets are each curved and are held against each other so that they go straight, one pushing and sliding against the other. However, when one stylet moves in front of the other the curve pushes the stylet in a lateral, sideways direction. Thus, the insect controls the direction in which it moves the stylets.



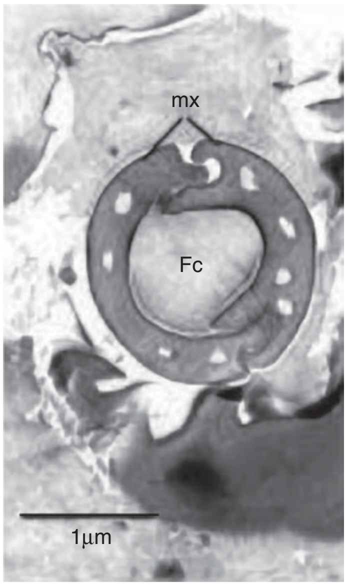
Plant Viruses and Insects, Figure 72 **Scanning electron micrograph (SEM) of the whitefly *Bemisia tabaci* showing the ventral surface. Body parts are as follows: C, compound eye; Clp, clypeus; Lbi, labium; Lbr, labrum; L, legs; St, stylet bundle.**

Some leafhoppers feed in a manner whereby they will pierce into the plant tissues and then proceed to feed in a clockwise or counter-clockwise procession, emptying cells as they go, thus creating an emptied out "spot" in the plant leaf, called a stiple. Others feed directly from the vascular tissues of plants, the phloem or xylem.

All these insects have piercing-sucking mouthparts that allow them to feed on plants while causing minimal damage. This is important for virus transmission, as viruses require a living cell to reproduce. The insects use paired maxillary stylets to form a suction tube that is inserted into plant cells, similar to a flexible syringe needle. In the Hemiptera, these stylets form two canals, the food canal, and a smaller salivary canal where the saliva of the insect comes out during feeding. The Thysanoptera are unique in that thrips stylets form a single canal used for both sucking up plant fluids and to secrete saliva. The insect salivary secretions have several functions. There are at least two types of saliva, one is liquid and aids in the digestion of plant cells and cell debris so that they



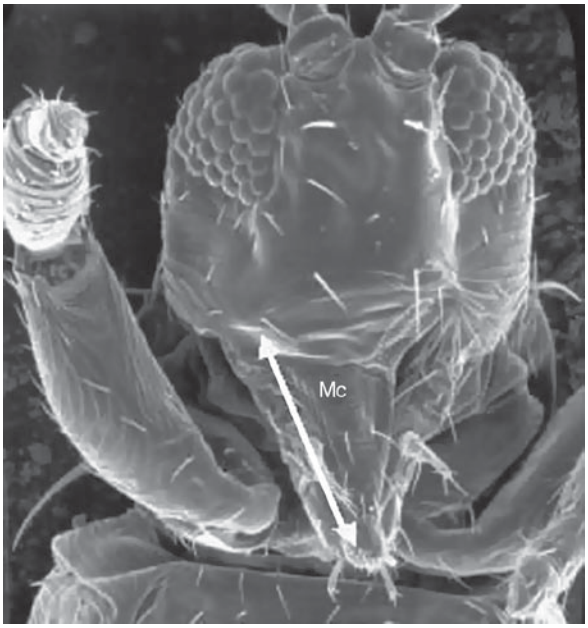
Plant Viruses and Insects, Figure 73 **Cross section showing stylets of a whitefly, with separate food and salivary canals: *Dc*, dendritic canal; *Fc*, food canal; *Md*, mandibular stylet; *Mx*, maxillary stylet; *Sc*, salivary canal.**



Plant Viruses and Insects, Figure 74 **Cross section showing stylets of a thrips, with single canal used for salivation and food intake: *Fc*, food canal; *Mx*, maxillary stylet.**

can be ingested, sucked up through the food canal. Another solidifies or hardens during feeding which functions to form a salivary sheath to help prevent leakage around the inserted stylets, and to hold the stylets firmly in place during feeding. The saliva also is thought to prevent or hinder the plant's response to repair its damaged cells so the insect can continue feeding once it finds the desired location inside the plant (i.e., the phloem or xylem).

There are also mandibular stylets. These are paired, thicker stylets on the outside of the maxillary stylets. The aphids, leafhoppers and whiteflies all have symmetrical, paired, matching mandibular stylets which function to pierce the hard epidermis of plants and to assist attaching the insect firmly to the plant surface. Only the thrips have an asymmetrical morphology with one of the mandibular stylets being reduced or absent, and the remaining stylet being closed at the end, forming a needle-like structure, closed at the end (Fig. 75). The thrips use the single, mandibular stylet to pierce a hole into the epidermis of the plant surface so that the slender, paired maxillary stylets can be inserted to feed in a piercing-sucking manner from plant cells that are deeper.



Plant Viruses and Insects, Figure 75 **Scanning electron micrograph of a thrips showing the face and mouthparts: *Mc*, mouthcone.**

By being able to feed in such a precise and direct manner, insects that feed in a piercing-sucking manner can avoid many of the plant's natural defenses. These insects also can deposit viruses directly into specific tissues from which they feed, such as into the vascular tissues of a plant. Once a virus has been introduced into the vascular tissues, it can spread rapidly throughout the plant to cause disease. Furthermore, piercing-sucking feeders cause less damage to the plant than a chewing insect, so plant cells that are infected with a virus often survive the feeding and support virus survival within the plant.

Inside the head there are several valves whereby the insects can stop the procession of food into their midgut. The plant sap is drawn up the food canal of the maxillary stylets. The food is then held in place by the precibarial valve where it is tasted by gustatory sensilla. The food is then drawn into the cibarium, the pumping chamber of the mouth. The cibarium also has gustatory sensilla for tasting and evaluating the quality of the food as the insect sucks up the plant sap. The food then passes the esophageal valve and enters the esophagus and passes through to the midgut which is the area of the alimentary tract where most nutrients are absorbed. In most plant sap-feeding insects, there is a region of the midgut where the hindgut coils around and is attached to it. This is the filter-chamber region of the insect's alimentary canal. Plant phloem and xylem, the liquids within plants' vascular tissues, are full of water; insects which feed on these as a primary food source have adapted over time the ability to shunt or direct excess water directly into the hindgut. This allows the insect to concentrate food and nutrients in the midgut for maximum absorption and to release excess water without having to process it through the midgut.

Tools to Understand Feeding (Electronic Monitoring of Insect Feeding)

Scientist have many methods to study insect/virus interactions. One such method is the invention of an electronic feeding monitor system, EMS, that allows someone to measure aspects of feeding as they occur. This is very important in studies where the amount of time an insect spends feeding needs to be measured. The EMS allows the scientist to know how many times an insect inserts its stylets into a plant, how long the insect fed, and if the insect was feeding from the phloem or xylem tissues within the plant. Being able to examine insect feeding so closely enables the early selection of crop varieties that may have resistance to insect feeding before they are planted in the field. Plant varieties which can disrupt insect feeding may be useful to prevent the transmission of some virus diseases. The EMS works by running a low voltage of electricity through a plant, usually by placing a copper electrode into the moist soil of a potted plant. The insect then has a fine gold wire glued onto its back, using electrical-conductive paint, so that the electricity will pass up through the plant, and then through the insect when it inserts its stylets into the plant. When the insect either salivates out, or ingests plant fluids up the food canal, the electricity passes through the insect, which acts as a variable resistor, and goes back into the EMS, which then amplifies the signal so that it can be recorded.

Insect Vector–Plant Pathogen Interactions

There have been two systems of terminology established to describe the association and transmission of plant diseases by insect vectors which feed in a piercing-sucking manner. One is based on how long the virus persists in the insect vector, and the second is based on the route of virus movement through the insect vector. They can be combined as follows: (i) the non-persistently transmitted, stylet-borne viruses; (ii) the semi-persistently transmitted, foregut-borne viruses; (iii) the persistently transmitted, circulative viruses; and (iv) the persistently transmitted, propagative viruses. Using this terminology, virus "transmission" is referred to as "non-persistent," "semi-persistent," or "persistent".

The way a virus moves through the insect vector then is described by the terms: "circulative" or "propagative." Circulative viruses pass into the insect hemolymph and circulate through the insects before being salivated back out during feeding. This involves the ability of the virus to pass several barriers within the insect, passing through the midgut membranes, and then the salivary gland membranes, to be able to be released back out with the saliva. These types of viruses do not replicate inside their insect vectors but merely pass through the insect. Viruses that reproduce inside the insect are considered propagative. Propagative viruses are able to enter the insect hemolymph but they also replicate once they infect an insect. As one would expect, a virus that is circulative is retained in the insect for a longer period of time than a virus that is non-circulative and merely stuck to the insects' stylets (stylet-borne) or foregut (foregut-borne virus). Viruses that are propagative (replicating in the insect) are retained for the life of the insect.

Non-persistently transmitted, stylet-borne viruses are transmitted into the plant during short durations of feeding. Virus acquisition (the ingestion of a virus that results in the insect's ability to transmit the virus to a plant), is brief, often just a few seconds of feeding. There is no latent period (the time that passes between when the virus is acquired and when it can be transmitted to a plant). Since these types of viruses usually are binding to the insect's stylets for only a brief period of time, the insect does not retain the ability to transmit the virus for long periods. Usually, virus transmissibility is lost after a few minutes of feeding on a non-infected plant. Aphids transmit the majority of non-persistently transmitted viruses. The ability of viruses to bind to the insect's stylets is aided by a helper component (a virus encoded, non-structural protein produced only in infected plants). During subsequent periods of feeding the virus is released, or washed from the stylets, thus depositing virus into the plant tissues.

Semi-persistently transmitted, foregut-born viruses are transmitted into the plant during longer durations of feeding (minutes). Virus acquisition increases with increased time spent feeding (minutes to hours), and the virus stays in association with the insect for several hours, being able to be transmitted into other plants. The virus is thought to be binding in the anterior areas of the alimentary tract, along the stylets to the foregut, and a few virus particles are released during each act of feeding. There is no latent period, the virus does not replicate, and the insect will lose the ability to transmit the virus during its life.

Persistently transmitted, circulative viruses do not replicate in the insect vector. These types of viruses are acquired and transmitted during long periods of feeding (minutes to hours), and there is a latent period of hours to days before the virus can be transmitted to another plant. This makes sense as the virus must move through the insect body and get into the salivary glands to be salivated back out before transmission can occur. Virus retention is long, but is dependent upon the amount of virus acquired into the insect body, and may last for the life of the insect, usually around 30 days.

Persistently transmitted, propagative viruses do replicate inside the insect. Virus acquisition time takes hours to days of feeding. The latent period can take weeks before an insect can transmit virus. The virus is retained for the life of the insect and often the virus is passed to the eggs (transovarial transmission).

Some Insect-Transmitted Viral Plant Diseases

Aphids

Of all known aphids, about 250 are considered serious pests. They are pests because of their feeding, which reduces the vitality of the crops they feed on, but primarily due to the transmission of viral plant diseases. Perhaps the most important aphid pest is *Myzus persicae*, often referred to as the green peach aphid. *M. persicae* is a green or slightly reddish aphid which has peach as its primary host and a wide range of secondary hosts, including many brassicas. *M. persicae* is cosmopolitan in temperate climates occurring in the U.S.A., and a fair portion of Europe including the United Kingdom. Though it seldom occurs in numbers large enough to cause direct damage from feeding pressure, it is capable of transmitting and spreading over 100 viruses including the potato leaf roll, potato virus Y, yellow net and yellows viruses of sugar beet, cauliflower mosaic, plum pox, cucumber mosaic, lettuce mosaic, and turnip mosaic virus.

The pea aphid, *Acyrthosiphum pisum*, is a large green aphid with long antennae and legs. The pea aphid is found on many leguminous plants and transmits Lucerne mosaic virus, pea leaf-roll virus, pea enation mosaic virus and pea mosaic virus in the United Kingdom, and pea enation mosaic virus in the U.S.A. The cabbage aphid, *Brevicoryne brassicae*, is a serious pest of the major cabbage crops, cabbages, cauliflowers and Brussels sprouts. The main cause of its pest status is the transmission of cauliflower mosaic and turnip mosaic virus. The brown citrus aphid, *Toxoptera citricida*, is a dark, black, aphid that is the main vector of citrus tristeza virus in the subtropics and tropics. The melon aphid or cotton aphid, *Aphis gossypii*, also is an important aphid vector of viral diseases in citrus and on many other agricultural crops.

The control of aphid pests currently still involves large amounts of pesticides in most countries, but other more ecologically friendly methods have been used in other places for some time. These generally involve biological control, mostly the use of *Hymenopteran parasitoids*. These are small wasps that lay their eggs inside the aphids. Other methods include plant improvement, and monitoring aphid dispersal to predict when a pre-emptive spraying in smaller amounts might be effective. The most important element of insect pest control for all of us is education. Farmers as well as the general public need to become better informed as to the alternatives to, and proper uses of, insecticides.

Leafhoppers

A large group of plant viruses, the plant rhabdovirus group, consists of more than 70 members. They are transmitted by aphids, leafhoppers, planthoppers, lacebugs, and mites. These viruses infect and replicate in the insect cells, but each virus is specific to its insect vector. Some of them also can be transmitted mechanically, through artificial means using plant sap from infected plants. Another important leafhopper-transmitted virus is maize chlorotic dwarf virus (MCDV). This virus is a semi-persistently transmitted, foregut-borne virus, and is restricted to the phloem of maize. Transmission of this virus requires a protein that is produced by virus-infected plants. This protein, called the helper component (HC), is suspected to bind to receptor-like structures in the food canal of leafhoppers, thereby forming a matrix to which virus particles attach. Viruses are then slowly released from this matrix during feeding and, consequently, are transmitted to other plants when leafhoppers fly to neighboring plants and then feed. The insect vector of maize chlorotic dwarf virus is the leafhopper, *Graminella nigrifons*.

The beet leafhopper (*Circulifer tenellus*) is one of the most important insect pests of sugarbeets in the western United States because it is the vector of beet curly top virus, BCTV. Curly top virus is a severely devastating plant virus that affects more than 300 broad-leaved plants. Tomato, bean, squash, cucumber, melon, spinach, table beet, pepper, and some flowering plants are the most common cultivated plants affected in the western United States. Leafhopper populations survive on weeds and cultivated plants infected with curly top virus which serve as reservoirs for both the insect and virus. Leafhoppers are able to acquire the virus during very short feeding times. The leafhopper retains the ability to transmit BCTV for a month or more after acquisition.

Whiteflies

In the past decade, whiteflies as pests and vectors of plant viruses have become one of the most serious crop protection problems in the tropics and subtropics. Yearly losses are estimated in the hundreds of millions of dollars. Several species of whitefly cause crop losses through direct feeding, while others are important in virus transmission. *Bemisia tabaci*, for example, is the vector of African cassava mosaic, bean golden mosaic, bean dwarf mosaic, bean calico mosaic, tomato yellow leaf-curl, tomato mottle, and other *Begomoviruses* in the family Geminiviridae, affecting crops worldwide.

With the spread of an especially aggressive biotype of *B. tabaci* into the New World tropics (*B. argentifolii*), crop losses likely will continue to increase, resulting in higher pesticide use on tomatoes, beans, cassava, cotton, cucurbits, potatoes, sweet potatoes and other crops. There is an urgent need to develop integrated pest management systems aimed at reducing insecticide use and which will help re-establish the ecological equilibrium of predators, parasitoids, and microbial controls. Needed are crop varieties with resistance to the whiteflies, and/or to the whitefly-transmitted viral diseases.

This problem is manifested in the fact that whiteflies and the viruses they carry can potentially infect many different host plants, including agricultural crops and weeds. A pest problem on one crop, such as beans, cannot be tackled as a single problem, as neighboring crops or weeds also may be affecting the disease spread. The different viruses and forms of the whitefly also are difficult to identify, and/or separate on the basis of symptoms or morphology. Determining where the problems in food crops are coming from becomes almost impossible. Proper diagnosis of the problem depends on using sophisticated molecular techniques to characterize the viruses and whitefly vectors, followed by epidemiological work, usually based on dynamic modeling, to understand the incidence of disease spread.

Thrips

Thrips species in the genus *Frankliniella* are commonly referred to as flower thrips. The western flower thrips, *F. occidentalis*, has a worldwide distribution and is considered the primary vector of tospoviruses. Thrips feed on over 600 different plants and crops, especially on flowering plants where they also feed on pollen. Many thrips are pests of commercial crops due to their damage to flowers. Also, their feeding causes stunting, deformed and unmarketable fruits and vegetables.

Thrips in the genera *Frankliniella* sp. and *Thrips* sp. also spread plant diseases through the transmission of viruses such as tospoviruses. Tomato spotted wilt virus is the type member of the genus *Tospovirus* in the family Bunyaviridae. These enveloped viruses are considered among the most damaging of emerging plant pathogens around the world. Virus members also include the impatiens necrotic spot viruses, which infect many ornamental plants. Tospoviruses can kill plants or reduce yields of marketable fruits and vegetables (i.e., lettuce, tomato, peanut, watermelon and ornamental crops). To transmit tospoviruses, thrips must acquire the virus during the larval stage. Most thrips species overwinter as either adults or as pupae. A typical flower thrips generation time varies from between 7 and 22 days depending on the temperature. The eggs are about 0.2 mm long and reniform (kidney shaped); they take on average 3 days to hatch. Thrips have two larval stages, then go through a prepupal and a pupal stage. Adults take between 1 and 4 days to reach sexual maturity. The females of the suborder Terebrantia are equipped with an ovipositor which they use to cut slits into plant tissue into which they insert their eggs one per slit, while females of the suborder Tubulifera, which lack an ovipositor, lay their eggs on the outside surface of plants, either singly or in small groups.

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Plasmatocyte

A common type of hemocyte capable of phagocytic, encapsulation and secretory functions.

► Hemocytes of Insects: Their Morphology and Function

Plasmid

Circular, dsDNA molecules found in bacteria that are often used in cloning. Plasmids are independent, stable, self-replicating, and often confer resistance to antibiotics. Often used in recombinant DNA work as vectors of foreign DNA.

Plasterer Bees

Members of the family Colletidae (order Hymenoptera, superfamily Apoidae).

► Bees

► Wasps, Ants, Bees and Sawflies

Plastron

Hairs or a tube-like process in which the cuticle of an insect or egg chorion holds a bubble of air through which gas exchange can occur while the insect is submerged in water. A physical gill.

► Eggs of Insects

Plataspidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Plate-Thigh Beetles

Members of the family Eucinetidae (order Coleoptera).

► Beetles

Platygastridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Platypezidae

A family of flies (order Diptera). They commonly are known as flat-footed flies.

► Flies

Platypodidae

Considered by some to be a family of beetles (order Coleoptera). They commonly are known as pin-hole borers. Here they are treated as a subfamily (Platypodinae) of Curculionidae.

► Beetles

Platystictidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Platystomatidae

A family of flies (order Diptera). They (and Otitidae) commonly are known as picture-winged flies, but Otitidae is now considered to be part of Ulidiidae.

► Flies

Pleasing Fungus Beetles

Members of the family Erotylidae (order Coleoptera).

► Beetles

Pleasing Lacewings

Members of the family Dilaridae (order Neuroptera).

► Lacewings, Antlions and Mantidflies

Plecomidae

A family of beetles (order Coleoptera). They commonly are known as rain beetles.

► Beetles

Plecomidae

A family of beetles (order Coleoptera). They commonly are known as rain beetles.

► Beetles

Plecoptera

An order of insects. They commonly are known as stoneflies.

► Stoneflies

Pleidae

A family of bugs (order Hemiptera). They sometimes are called pygmy backswimmers.

► Bugs

Pleiotropic

Term used to describe a gene that affects more than one, apparently unrelated, trait.

Pleural

An adjective describing the lateral region of an insect, or features found laterally.

Plesiomorphy

When considering classification and phylogeny, an ancestral or primitive character state.

Pleuron (pl., pleura)

The lateral plates of the insect body segments, especially the thoracic segments.

► Thorax of Hexapods

Plica

A longitudinal fold or wrinkle in the wing of an insect.

Plokiophilidae

A family of bugs (order Hemiptera). They sometimes are called web-lovers.

► Bugs

Plumaridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae)

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The plum curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), is an important pest of pome and stone fruit orchards in North America. The insect is distributed from Quebec to Florida, east of the Rocky Mountains and in Utah. Two strains are found: a northern and a southern strain, which have, respectively, one and two generations per year.

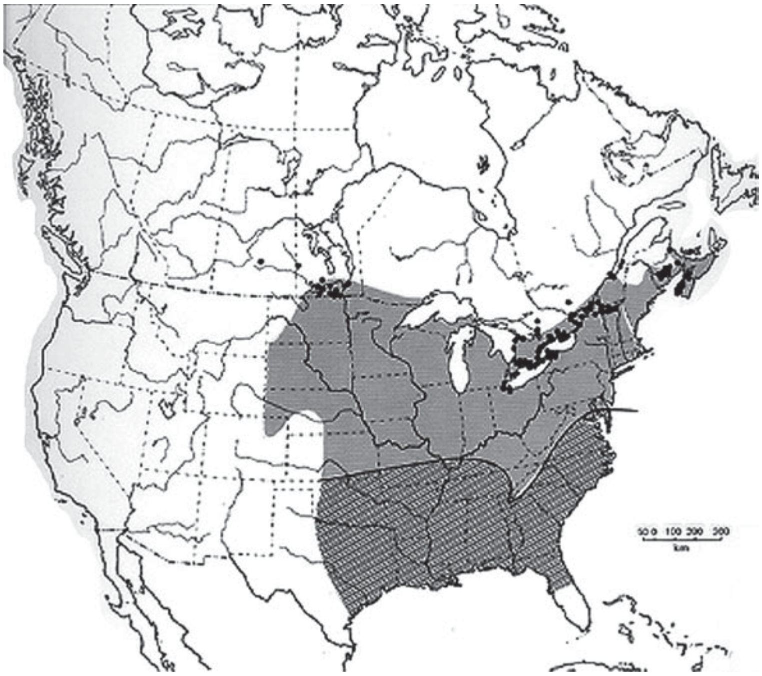
Life Cycle

C. nenuphar overwinters as adults in plant debris, preferably under maple leaves. The pest is univoltine in the northern part of its range (north of Virginia, USA) and at least partially multivoltine in southern areas including populations present in mid-Atlantic regions of West Virginia and New Jersey (Fig. 76). Spring emergence times vary with geographical location. In Quebec (Canada), overwintered adults emerge in late April when apple trees of cv. McIntosh reach the "green tip stage." Emergence reaches a peak from 6 days before full bloom to 10 days after petal fall. In southwestern Quebec emergence may take 3–4 weeks to complete. In Ontario (Canada), emergence begins at end of April and is nearly complete by early June, but continues until late June or early July. In Texas, emergence occurs from late March to early May. Adults begin to emerge and become active when mean daily temperatures reach approximately 13–15°C.

After emergence, adults remain on the surface of the soil for some time before appearing on the trees, where they feed on the new shoots and blossoms until fruit becomes available. In spring, adults invade orchards mainly from the surrounding woodland. In Quebec, the adult population peaks somewhere between the tight cluster stage and 10 days after petal fall on apple. The highest distance covered by the adults, mainly by walking, was recorded from the tight cluster stage until physiological fruit drop in late June. In southern regions in the United States, adult populations on peach and plum peak at least 1 month earlier.

In Ontario, oviposition begins in late May and continues until early August. The timing of oviposition varies with climate. In New York State, it was estimated that 60% of total fruit damage by oviposition is accomplished when 230 day-degrees (above 10°C) had accumulated after petal fall in apple (mid-June on average in that region).

Eggs are laid in an epidermal cavity in the fruit that the female excavates. The skin is cut into a distinctive crescent-shaped slit, which partially surrounds the egg. The eggs and young



Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), Figure 76 **Distribution of plum curculio in North America. The map shows the area inhabited by both the northern (single generation per year) and southern (more than one per year) strains.**

larvae are sensitive to internal pressure and other unfavorable effects of fruit growth. Eggs crushed by rapidly growing apple fruit may account for varietal differences in the susceptibility to attack by *C. nenuphar*. The gum exudate from egg-laying scars on half-grown plums can kill the larvae. More than one larva can develop in a single fruit. The abundance of fruit has a significant influence on *C. nenuphar* population dynamics and a poor crop may lead to a marked decrease in population size. The larvae feed in the fruit, which usually drops prematurely unless egg or larval development is interrupted in its early stages. The time spent in the fruit varies from 15 to 18 days. When fully fed, the larvae leave the fruit and pupate in cells in the soil. The time spent in the soil depends on temperature and humidity but varies from 3 weeks to more than 5 weeks, the longer periods generally occurring in the northernmost part of its range.

The summer generation of adults emerges over a long period from July to October in Ontario, and Maine, with a peak of emergence in September. In Georgia, approximately 50–75% of females lay eggs in the same year, giving a partial second generation. The adults leave the trees and search for overwintering sites in September and October. In caged experiments in Quebec, 93% of adults overwintered at the soil surface under leaves and other debris, 4% were found in the top inch of the soil and the remainder overwintered deeper in the soil. In Virginia, weevils were found hibernating up to 15 cm deep in loose soil and in clay, at an average depth of 6 cm.

Host Plants

Plums, peaches, apricots and nectarines are the preferred hosts of *C. nenuphar*, but apples are also widely affected. Other economically important hosts include sweet cherry, sour cherry and blueberry. Apples are less damaged in areas adjacent to peach orchards than in areas where peaches are not grown. Peaches are often scarred and deformed by the feeding and egg punctures of *C. nenuphar*, with larvae developing successfully and leaving the fruit to pupate. There are varietal differences in the susceptibility of apples, with eggs being destroyed and larval establishment being prevented by fruit growth in some cultivars.

Damage and Economic Impact

Second only to the codling moth (*Cydia pomonella*), *C. nenuphar* is regarded as the most serious pest of pome and stone fruit in eastern North America. For example, in Quebec up to 85% of harvested apples may be damaged by *C. nenuphar* in unsprayed orchards. Plum curculio damage returns to levels of economic importance 1–3 years after cessation of pesticide spraying.

On apple, *C. nenuphar* can cause three types of external damage. In spring, males and females feed on, and females oviposit in, young fruit, leaving behind small round feeding punctures and marking them with characteristic half-moon shaped scars (Fig. 77), respectively; and in spring and summer, the adults puncture the fruit causing round (2–3 mm diameter), feeding scars (Fig. 78).

Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), Figure 77 Oviposition scar on the surface of an apple.

Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), Figure 78 Adults and feeding punctures on young fruit.

The appearance of plum curculio damage is highly variable and, of all fruit damage rated by IPM specialists, damage caused by plum curculio had the lowest agreement level, i.e., 71.8%. Internal damage to the fruit is caused by larval feeding and exit holes. Most infested fruits drop prematurely in June, though cherries rot on the trees. Larvae release pectic enzymes and cellulase while they feed internally aiding in fruit abscission. Adult feeding may also cause marginal damage to leaves and blossoms.

Management of the Plum Curculio

Insecticide treatments are usually recommended against the adults at petal fall and once or twice thereafter at 10- to 14-day intervals. No resistance to synthetic insecticides has yet been reported for this pest. Alternatives to insecticides are discussed hereafter.

Behavioral Studies

Observations on the behavior of adults, both in the field and in cages, Using Zn^{65} as a marker to track adults has led to the design of better IPM programs for plum curculio. In autumn, most adults labeled with Zn^{65} moved from orchards to surrounding woodlots. After overwintering, the returning plum curculios gradually invade adjacent apple orchards between pink and petal fall, after spending several days on the ground under the perimeter rows of trees, which most of them then climb. From full bloom to 9 days after fruit set, plum curculio adults were found to be active mainly during the night. In field cages, adults labeled with Zn^{65} also showed a similar diel periodicity while foraging on dwarf apple trees. Because adults are most active in the trees at night, it is recommended that insecticide treatments are likely to be most effective if applied during the first hours of darkness.

There have been several attempts to relate adult activity to ambient temperature in order to optimize the timing of insecticide treatments. Two approaches have been investigated: the development of a trap to evaluate adult populations and establish a relationship between population levels to risks and the development of day-degree models to predict the appearance of damage in orchards. Neither of these methods has been used in isolation to manage populations of *C. nenuphar*. A model predicting the nocturnal activity of *C. nenuphar* hourly has recently been developed and is currently under validation.

Treatment of Peripheral Zones of Apple Orchards

The strategy to treat 20 m-wide peripheral zones of apple orchards (when needed) in spring is based on the fact that plum curculio damage is frequently more abundant at this time in peripheral zones, and that during the tight cluster stage most plum curculio adults move only 1–4 m/day when returning to the orchards from their overwintering sites in adjacent woodlots. During this 5–20 day reinvasion period in southern Quebec, petal fall appears as the most appropriate time for a peripheral zone treatment.

Using this approach in a 1.7 ha experimental orchard (with standard-size trees) in Quebec, fruit damage at harvest was reduced from 57 to 2.4%, while reducing the amount of insecticide used by 70%, and the plum curculio adult population by 83%. These results were consistent over a 2-year period in one locality, under high population pressure. The mortality data were based on recaptures of plum curculio adults, radio-labeled with Zn^{65}, that had been released in a woodlot adjacent to an orchard in which the peripheral zones had been treated with insecticides.

Peripheral-zone spraying has been validated in commercial orchards and compared for effectiveness with full-block spraying in four commercial apple orchards in southern Quebec. Plum curculio damage at harvest was less than 0.7 and 0.8% fruit in plots receiving peripheral and full-plot sprays, respectively; and most damaged apples (95%) were found in peripheral zones.

Trapping Methods

The best (although tedious) monitoring method available for plum curculio in commercial orchards still remains careful examination of thousands of small fruit to detect fresh egg-laying scars. In Quebec a threshold of 1% damaged fruit, based on careful monitoring of fruit three times a week, was successfully used for managing localized peripheral zone treatments following full-block treatment at petal fall. A lower threshold and daily monitoring would be required, however, in areas where the pest pressure is very high. Limb tapping as a monitoring technique is not popular with growers because beating sticks damage the trees, and accuracy varies with cultivar, tree shape, time of day and scout experience.

There have been several studies aimed at improving the timing of insecticide treatments by monitoring adult plum curculios with traps designed for other curculionids or with novel trapping methods. Inverted polyethylene funnels have been evaluated by hanging them beneath tree trunks to capture falling adults. Unbaited sticky-coated green plastic spheres (3 and 8 cm diameter) and sticky-coated green thinning apples (3 cm diameter) hung in host trees, PVC pitfall traps placed beneath host trees, 5 cm bands coated with a sticky substance encircling tree trunks, and unbaited and baited (baited with boll weevil pheromone, grandlure) boll weevil traps placed on vertical stakes between woods and commercial orchards have also been tested. However, no plum curculios were captured on sticky bands and very few were captured in pitfall and boll weevil traps. Black pyramid traps placed next to apple tree trunks, originally designed to mimic the visual silhouette of the trunk of a pecan tree and used to monitor pecan weevil, *Curculio caryae*, captured significantly more plum curculios than those traps placed between apple trees, between apple trees and an adjacent wood lot, and between apple trees and an adjacent field.

However, occurrence of plum curculios in these pyramid traps did not coincide with temporal occurrence of ovipositional injury nor did number of adults captured coincide with levels of ovipositional injury, possibly because of abiotic factors. In experiments designed to learn how plum curculios move into host fruit trees, adults dislodged from apple trees tended to walk off a small collecting frame when ambient temperatures were below 20°C, but fly to a host tree canopy or inter-tree space when temperatures were 20°C or above. This indicates that plum curculios are likely to bypass any sort of trap designed to intercept crawling individuals such as black pyramid traps placed next to tree trunks when temperatures are above 20°C. Therefore, traps that capture flying plum curculio adults as they enter the orchard or after arrival in the host tree canopy also have been evaluated. Clear Plexiglas panels have been evaluated for their ability to intercept flying adults. The circle trap consists of a wire screen cage capped with an inverted screen funnel and attached to a limb; it is designed to intercept foraging adults walking on tree limbs or on the tree trunk, and not to attract adults based on stimulating visual cues. A third trap type that has been evaluated in host tree canopies is the branch-mimicking cylinder trap, designed to exploit visual cues provided by an upright twig. So far, none of these unbaited trap types have shown sufficient attractiveness or reliability to replace the visual examination of fruitlets as the recommended monitoring technique. However, addition of attractants to trap types is considered to be the next logical step for their improvement.

Attractants

Numerous species of weevils are attracted to host plant volatiles or specific compounds present in host plant volatiles, including the banana weevil, *Cosmopolites sordidus* (Germar), the cabbage seed weevil, *Ceutorhynchus assimilis* (Paykull), the pea weevil, *Sitona lineatus* (L.), and the red weevil, *Rhynchophorus ferrugineus* F.

Attempts to identify potential attractants for adult plum curculios were first published in the 1920s. It was reported that adult plum curculios are attracted to salicyl-aldehyde early in the season and gallic acid later in the season. More recently, much effort has focused on identification of potential attractants. In the 1980s, fresh apple juice and synthetic apple blossom fragrance were evaluated, and in the 1990s stored apples, fresh apple branchlets, and ammonium carbonate as potential attractants were also evaluated: all proved unsuccessful. Chemically uncharacterized host apple odor from water- and hexane-based extracts was most attractive between bloom and 2 weeks after bloom. Furthermore, volatiles released from punctured plums were very attractive to plum curculios in laboratory bioassays. Specific compounds identified from plum and/or apple volatiles and found to be attractive to plum curculio as evidenced by laboratory and/or field bioassays include ethyl isovalerate, limonene, benzaldehyde, benzyl alcohol, decanal, E-2-hexenal, geranyl proprionate, and hexyl acetate. Because odors of host fruit were significantly less attractive at 4 and 8 cm than at 2 cm from plum curculios, fruit odor-based traps may not be useful in commercial orchards. However, host plant volatiles often synergize or enhance insect responses to sex and/or aggregation pheromones. In the family Curculionidae, male-produced pheromones have been documented in at least 21 species and enhancement of attraction to them by the presence of host plant volatiles have been documented in at least 18 species.

Some antennal sensory structures on plum curculio are similar to pheromone receptors found on related curculionids. Researchers recently isolated and subsequently synthesized an aggregation pheromone from male plum curculios: (+)-(1R,2S)-Methyl-2-(1-methylethenyl) cyclobutaneacetic acid. This pheromone, which they named grandisoic acid, is attractive to both sexes. Attempts to use live adults in pyramid traps were unsuccessful, baited traps being no more attractive than unbaited traps, possibly because of repulsive distress signals emitted by the curculios. However, lures impregnated with a racemic mixture of grandisoic acid have been reported to significantly increase the number of plum curculios trapped in pyramid traps. A two-fold increase in attractiveness when the lure was used in conjunction with small amounts of green leaf volatiles; high amounts showed a repulsive effect. More recently, it has been demonstrated that pyramid and sticky Plexiglas panel traps baited with a combination of grandisoic acid and benzaldehyde and placed close to woods and adjacent to orchards, captured more immigrating plum curculios than grandisoic acid alone or unbaited traps. This combination of attractants has been deployed within apple tree canopies to aggregate plum curculios and to monitor seasonal activity. This monitoring technique is termed a “trap free” approach.

Biological Control

Several natural enemies have been recovered from *C. nenuphar* but none are able to provide an effective alternative to chemical insecticides in commercial orchards. Several nematode species have been tested and found to be effective as larvicides against *C. nenuphar*. In the laboratory, 95% larval mortality was reported at 400 *Steinernema carpocapsae*/larva. At 200–400 nematodes/larva, 73.4% larval mortality was achieved in natural sods. Nematode treatments would also affect other pests, such as the larvae of *Hoplocampa testudinea* (apple sawfly). The application of nematode treatments to the soil would not prevent damage to apples, but would lower *C. nenuphar* and *H. testudinea* populations for the subsequent growing season.

Repeated applications of *S. carpocapsae* to the foliage or aerial parts of apple trees were tested to prevent damage to the fruit. In caged environments, localized application of nematodes at the base of tree trunks significantly reduced adult populations (82–100% mortality).

► Apple Pests and Their Management

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Plume Moths (Lepidoptera: Pterophoridae)

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Adult plume moths are generally small, with wingspans of about 2 cm, but range from 6 to 40 mm. They are easily recognized by their characteristic T-shaped resting posture with the narrow forewings held perpendicular to the body and the hindwings tucked under or folded within the forewings. The wings are often divided into lobes, or plumes, with long fringe scales accentuating the feather-like appearance (Figs. 79–81). The fore- and hindwing are typically divided into two and three lobes, respectively, but one subfamily, Deuterocopinae, has one or two additional clefts in the forewing, and the subfamilies Agdistinae and Ochyroticinae have both wings entire. Many species are plain white or mottled gray or brown. Others are more striking, with banded legs, scale tufts at the tibial spurs, and wing maculation that includes clusters of spatulate scales mixed within the linear fringe scales. Worldwide, 1,139 species and 92 genera are reported in the most recent world catalogue, with at least another 300 new species anticipated, especially from tropical regions. The group has been divided into four or five subfamilies by different authors. Genera of the subfamily Platyptiliinae have been recently included within the Pterophorinae.

Morphology and Family Characters

Adults

Aside from cleft wings, the primary defining character for the family, present in all genera and species, is rows of stout sclerotized scales arising from the underside of the hindwing median and cubital veins. These scales were once referred to as androconial scales, but occur in both males and females, and have since been termed venous scales. There are no apparent openings in these scales and their functional significance, if any, is still unknown. The Macropiratidae, generally accepted as the sister taxon to the pterophorids and treated as a subfamily of Pterophoridae by some authors, do not have venous scales. Pterophorid hind legs are proportionally long, most with two pairs of enlarged tibial spurs. The hind legs are not used for grasping but are held against the abdomen or away from the body at an angle similar to most Heliodinidae, Schreckensteiniidae, and stathmopodine Oecophoridae. The abdomen is long and narrow, with scale tufts often associated with the genitalia. Females have an eversible bilobed pheromone gland just above the ovipositor. Many species require dissection and preparation of genitalia slides for determination.

Immature Stages

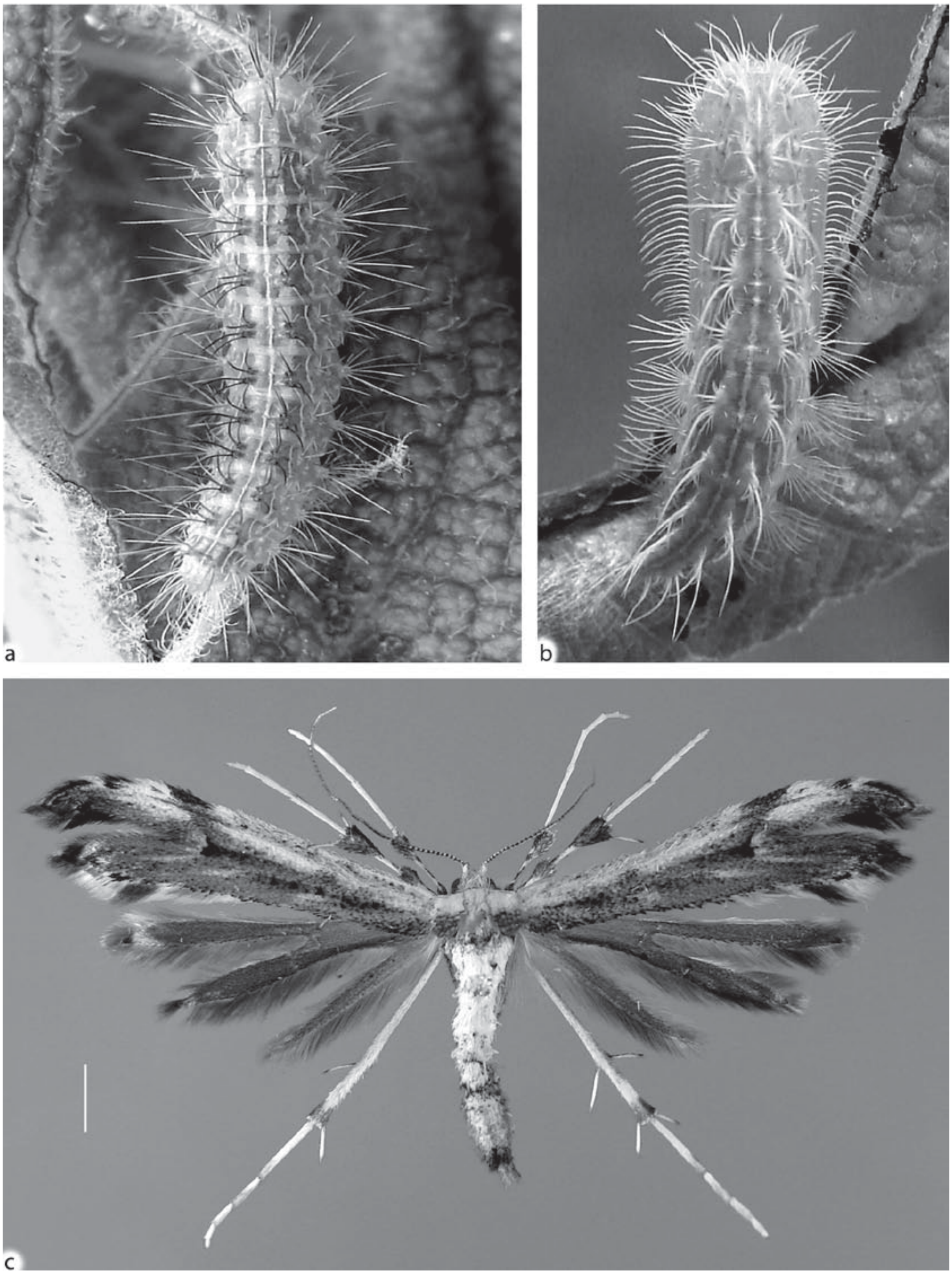
Eggs are oval to oblong, generally under 1 mm in length. The color varies by age and species but is usually white to yellowish or light green and they often appear glossy. The chorion surface is smooth, pitted, or finely reticulated.

Larvae of most species have secondary setae or spinules, subprimary seta L3 present on the prothorax, 2 SV setae present on all three thoracic segments, and crochets on the prolegs arranged in a uniordinal mesopenellipse. The prolegs are usually slender and peg-like, except in some of the borers. Larvae of external feeders are sometimes cryptic, with ingested plant material showing through the cuticle, or fairly easy to spot with contrasting longitudinal bands. The setae tend to be long, both primary and abundant secondary setae often blending in with the host-plant trichomes. Internal feeders are less colorful, either plain or cream-colored or with pink to red markings, with shorter and fewer secondary setae and shorter or reduced prolegs. Some internal feeders have sclerotized anal plates with thorn-like terminal structures. Secondary setae are localized, scattered, or radiate from verrucae or verruca-like tubercles, often with a distinct central primary seta. Setal morphology is diverse and quite remarkable, ranging from simple setae with pointed tips, to modified setae with spiculate or barbed margins, flattened scale-like setae, and apically modified setae with blunt, inflated, capitate, spatulate, tined, or conspicuously forked tips. In some genera including *Buckleria*, *Dejongia*, *Megalorhipida*, and *Trichoptilus*, inflated, or hollow, open-tipped glandular setae exude a viscous, sticky fluid, which accumulates in a droplet at the end of the seta.

Pupae exhibit a variety of shapes and some are fairly colorful. Many appear quite spiny, with secondary setae and tubercles carried over from the larval stage, including lateral verrucae (Fig. 79). In addition, fringes of secondary setae are frequently present along the lateral margin of the forewing and antenna. In several genera, dorsal abdominal tubercles are noticeably enlarged on the third abdominal segment. All pterophorid pupae have the first three abdominal segments fused, making movement only possible below the third segment. Related families, such as Macropiratidae, have the first four segments fused. Most species have two distinct patches of hooked setae or hamuli on the ventral surface of the tenth abdominal segment for anchoring to a silk pad spun by the larva.

Host Plant Associations

Pterophorid larvae feed on various plants representing about 70 different families. They are predominantly associated with the family Asteraceae (Compositae) with more than a third of the recorded hosts belonging to this family. Next to the composites, Lamiaceae are the second most common host family, with the whole order Lamiales including about 23% of the recorded hosts. The family Fabaceae or legumes also includes many hosts, especially in the tropics and subtropics. Other families with several hosts include Plantaginaceae, Convolvulaceae, Vitaceae, Rosaceae, Orobanchaceae,



Plume Moths (Lepidoptera: Pterophoridae), Figure 79 ***Oidaematophorus eupatorii*****: (a) larva, (b) pupa, and (c) adult. Line = 2 mm.**

Gentianaceae, Amaranthaceae, Dipsacaceae, and Plumbaginaceae. Certain pterophorid genera are strongly associated with specific host families or genera, while a few, such as the pantropical species *Sphenarches anisodactylus* (Walker), are polyphagous.

Distribution

Plume moths are found in all faunal regions and a range of different habitats extending to arctic and sub arctic zones of Greenland and Iceland, high elevations in the Alps where the genus *Stenoptilia* is diverse, and arid or saline areas where the genus *Agdistis* is well represented. While many species are restricted to certain regions or habitats, others such as the morning glory plume moth, *Emmelina monodactyla* (Linnaeus), are widespread and occur in several faunal regions. Species occurring in tropical and subtropical areas tend to have multiple or continuous broods.

Life Histories, Habits and Behavior

Adults

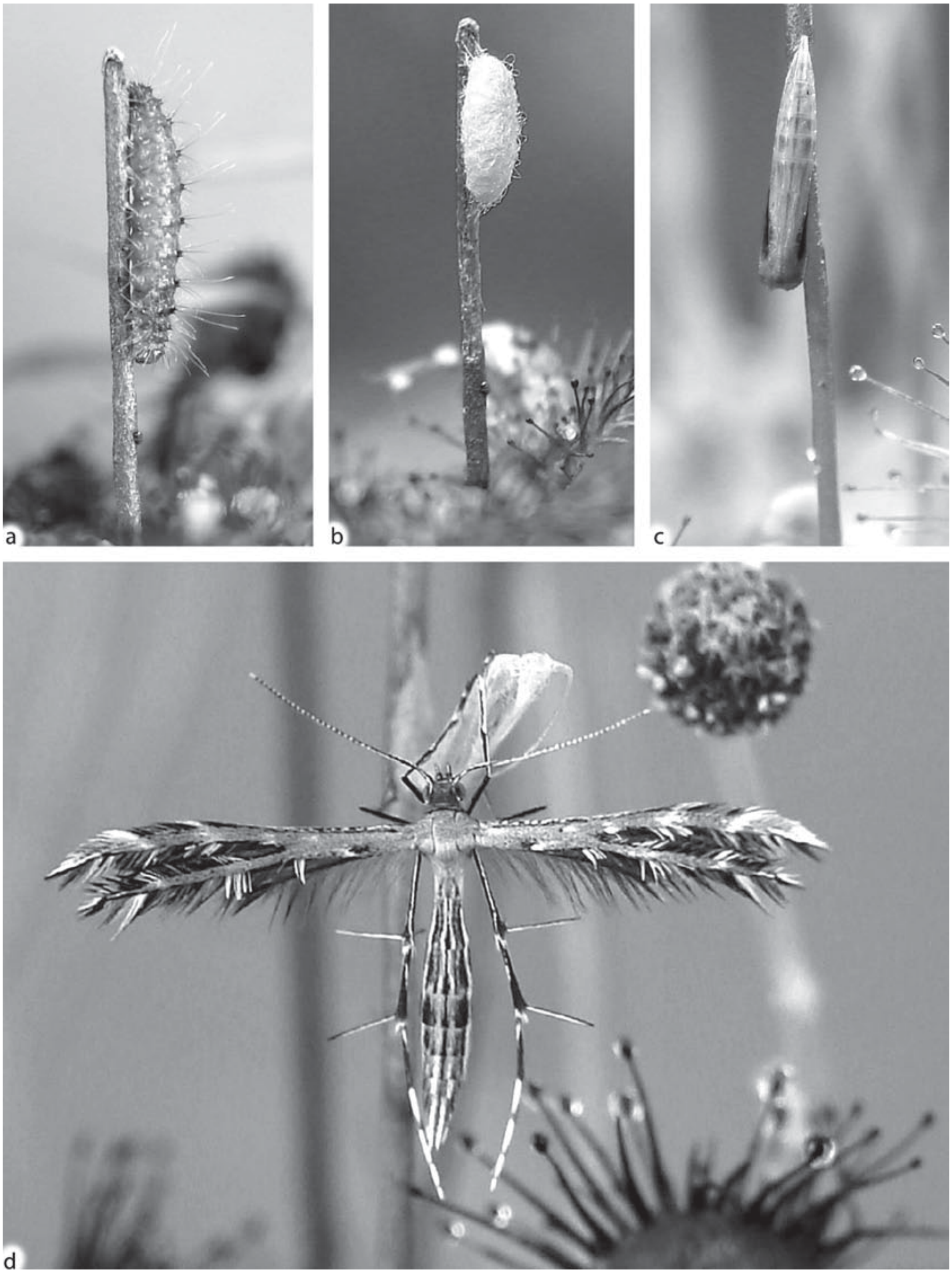
Plume moths typically fly for short distances before alighting and are easily tracked by day or followed with a headlamp at night. Adults are active early in the evening, at night, and may also be collected by sweeping or beating vegetation in shady areas during the day, or collected in the vicinity of larval hostplants. A few species actively seek nectar by day, even in sunlit areas. Both males and females are attracted to lights at night. Eggs are deposited singly or close together in loose groups, usually directly on the hostplant and in specific locations such as tender leaves, flower buds, or shoots where the first instar larvae will feed. In species where first instar larvae overwinter or diapause within the egg chorion, eggs may be placed on persisting structures such as at branch axils of woody stems.

Larvae

Pterophorid larvae exhibit a wide range of feeding habits which vary with hostplant species, growth stage, season, and availability of preferred plant parts. Certain species feed on whatever part of the host is available, while others are specialists, seeking out specific structures such as developing seeds or immature anthers within flower buds. Early instar larvae tend to feed on softer tissues, foliage feeders starting out on terminal shoots before consuming mature leaves. Stem borers such as the golden-rod borer, *Hellinsia kellicottii* (Fish) and the *Baccharis* borer *H. balanotes* (Meyrick) typically feed in shoots or flowers before re-entering the stem or branch lower to the ground, some feeding and hibernating in the lower stem and roots. Two species of *Adaina* are known to produce stem galls. Externally feeding larvae tend to initially resist movement when disturbed while internally feeding species, such as flower and stem borers react more readily when agitated, the stem borers quickly retreating to the lower extent of their burrows. Most are solitary feeders, with only one larva found per shoot, but a few, such as the common nearctic species, *Oidaematophorus eupatorii* (Fernald), are gregarious, with several young larvae webbing together the upper shoot and young leaves of species of *Eupatorium* (Joe-Pye Weed) (Fig. 79).

Sundew Plume Moths

The sundew plume moth (Fig. 80), *Buckleria parvula* (Barnes and Lindsey) (formerly *Trichoptilus parvulus* Barnes and Lindsey, 1921), is one of the most fascinating species because the larvae feed on the carnivorous plant genus *Drosera*. These plants have glandular trichomes that ordinarily trap small insects. Reaching only 8 mm in length, these tiny plume moth larvae ingest the sticky fluid at the trichome tips and will mow down a whole patch of these hairs before feeding on the rest of a leaf. Feeding mostly at night, in addition to leaves, larvae will also eat dead insects trapped by the leaves and crawl up the inflorescence stalks to feed on the flower buds. Larvae may be found resting on the undersurface of the leaves or on the inflorescence stalks during the day but are usually difficult to spot because their reddish color, especially in younger larvae, blends in with the plants (Fig. 80).



Plume Moths (Lepidoptera: Pterophoridae), Figure 80 Plume moths (Lepidoptera: Pterophoridae): (a) parasitized larva of the sundew plume moth, *Buckleria parvula*; (b) cocoon of *Cotesia* wasp spun by parasitoid larva emerging from the same moth larva; (c) pupa of sundew plume moth 12 h before emergence; (d) newly emerged sundew plume moth adult perching on pupal skin.

Plume Moths (Lepidoptera: Pterophoridae), Figure 81 Examples of economically important plume moths: rose plume moth, *Cnaemidophorus rhododactyla* (above); artichoke plume moth, *Platyptilia carduidactyla* (below). Line = 2 mm.

While successfully avoiding the peril of the sundew's sticky traps, larvae frequently fall prey to a species of *Cotesia* wasp (Braconidae). A single wasp larva emerges from the final instar pterophorid larva and immediately spins its cocoon, leaving the pterophorid crawling around for hours before it finally expires. In contrast to the moth larvae, the white cocoons of the parasitoid larvae are easily spotted on the *Drosera* leaves or inflorescences, and persist long after the wasp emerges after a pupal stage of about 6 days. Several spent cocoons may be found on a single plant. In some populations more than half the pterophorid larvae are parasitized.

The plume moth larvae that manage to avoid the wasps pupate on the inflorescence stalks or on nearby blades of grass and in this particular genus, are always positioned with the head facing down. The pupa is light green, changing to yellowish-tan and brown before emerging after up to 11 days. The newly emerged moth clings to the pupal skin while the wings, at first drooping at an angle, expand and are held fully erect, perpendicular to the body.

Buckleria parvula is found in the southeastern United States, with larvae collected from May to October on several different species of sundews. These plants grow in damp areas of pine flatwoods, bogs, lake shores, seasonal ponds, and drainage ditches with nutrient poor soil. Four other species of sundew moths are known, *B. paludum* (Zeller) from the Palearctic and Oriental Regions, *B. girardi* Gibeaux and *B. madecassea* Gibeaux from the Ethiopian Region, and *B. brasilia* Gielis from the Neotropical Region.

Economic Species

Most plume moths infest plants of little economic or cultural significance but a few are pests of crops, ornamentals, or are of value for the biological control of nuisance weeds. The artichoke plume moth, *Platyptilia carduidactyla* (Riley) is a well known pest of the globe artichoke, *Cynara scolymus* (L.) (Fig. 81). Larvae feed in the stems, shoots, and developing flower heads of artichoke in California, as well as native thistles throughout much of the Nearctic Region. Studies of the male calling pheromone produced by adult females have been an important component in control applications including traps for monitoring populations, mating disruption, and mass trapping. Also in the Nearctic Region, the grape plume moth, *Geina periscelidactyla* (Fitch), is a minor pest of cultivated grape, feeding and webbing together young leaves and shoots. This species is more commonly found on wild than cultivated grape species. *Geina sheppardi* Landry and *Sphenarches ontario* (McDunnough) also feed on certain species of wild grape, the larvae of both feeding on the inflorescences.

Some ornamental plant pests include the snapdragon plume moth, *Stenoptilodes antirrhina* (Lange) on *Antirrhinum*, the geranium plume moth, *Amblyptilia pica* (Walsingham) on *Pelargonium*, and the calendula plume moth, *Platyptilia williamsii* Grinnell on marigolds (*Calendula* spp.). Larvae of the rose plume moth (Fig. 81), *Cnaemidophorus rhododactylus* (Denis & Schiffermüller) feed on leaf shoots and flower buds of cultivated roses in temperate areas of the Palearctic and Oriental Regions. It was introduced from Europe to the northeastern United States sometime in the early 1800s. The wing maculation and banded legs of the adults make this one of the most attractive species, despite its minor pest status. The first instar larvae have the interesting habit of not feeding upon hatching but spinning tiny spherical silk hibernacula in which they overwinter.

Several pterophorids have been investigated as potential biological control agents of various weeds. Two European species have been introduced to Australia, *Wheeleria spilodactyla* (Curtis) to control horehound, *Marrubium vulgare* L., and *Platyptilia isodactyla* (Zeller) to control tansy ragwort, *Senecio jacobaea* L. *Hellinsia balanotes* has also been introduced to Australia from the United States for control of *Baccharis halimifolia* L. In Hawaii, *Hellinsia beneficus* (Yano & Heppner) was introduced from Mexico to control *Ageratina riparia* (Regel) R.M. King & H.Rob. The lantana plume moth *Lantanophaga pusillidactyla* (Walker) was likewise introduced from Mexico to control *Lantana camara* L. in Hawaii as early as 1902. A European species, *Agdistis tamaricis* (Zeller) is under consideration as a potential control agent of saltcedar, *Tamarix ramosissima* Ledeb. in the southwestern United States.

► Butterflies and Moths
► Insectivorous Plants

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Plumose

Feather-like structure with a single thick stem and numerous parallel branches. This term usually is used to describe the antennae of Lepidoptera.

► Antennae of Hexapods

Plutellidae

A family of moths (order Lepidoptera). They commonly are known as diamondback moths.

► Diamondback Moths
► Butterflies and Moths

Poduridae

A family of springtails (order Collembala). They commonly are known as water springtails.

► Springtails

Poikilothermic

Cold-blooded animals; animals (including insects) that lack an internal temperature regulation system, and so tend to have body temperatures that mirror the temperature of their environment. Poikilothermic animals actually use behavior and heat generated by muscles to adjust their temperature to some degree (contrast with homeothermic).

Polar Filament

A hollow, thread-like organelle associated with a microsporidian spore that extrudes, and allows the sporoplasm to pass to the exterior and to inoculate a cell.

Pollen Basket

A specialized scopa, or pollen holding apparatus, found in bumble bees and honey bees. The pollen basket consists of the broad, concave hind tibia surrounded by a fringe of long hairs. *A. corbicula*.

Pollenose

Covered with a loose, dusty yellow material resembling pollen, and which can be rubbed off the surface of an insect.

Pollen Pot

A container made from soft cerumen by stingless bees, and used to store pollen.

Pollen Rake

A comb-like row of bristles at the tip of the hind tibia of bees.

Pollination and Flower Visitation

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Insects are the most common and abundant pollinators of flowering plants, far surpassing the other winged pollinators, the birds and bats. Other insects (anthophiles) visit flowers but do not necessarily pollinate them. The history of the relationships between insects (both pollinators and anthophiles) and flowers is long and varied. Their modern-day importance in ecosystem functioning and agricultural production has made them the subject of numerous scientific studies.

Evolutionary Overview

The relationships of insects and the sexual reproductive organs of plants may be as ancient as the insects and terrestrial plants themselves. Such relationships probably preceded pollination to a time before pollen existed. The first terrestrial plants produced unicellular spores that may have been food for the first terrestrial insects, probably Collembola. Thus, some 400 million years ago in Devonian time, *Rhyniella* (Collembola) and its relatives may have consumed the spores of *Rhynia* and its relatives (primitive vascular plants known only from fossils). Other arthropods have been found in association with the sporangia of plants of that time also. By the time the Carboniferous forests dominated major parts of the globe, insects were well represented in the fauna. Several extinct orders are known to have had elongated mouthparts, reminiscent of those associated today with insects that suck liquids from tubular structures, such as flowers. Moreover, spores (microspores) have been found associated with those insects, particularly on their mouthparts and their wing bases. Reproductive organs of the plants of the Carboniferous, and earlier, had structures (bracts) that formed tubes leading to the micropylar droplet (the germination medium for the microspores) above the megaspore retained on the parent plant. By mid-Mesozoic, some cycadoid gymnosperms appear to have had apparently showy structures embracing the sexual sporangia. Thus, a firm trend towards the insect-plant mutualism of pollination seems to have roots extending into the past well before the advent of the Angiospermae (the flowering plants), a Cretaceous phenomenon of some 160 million years ago.

Insect pollination is generally thought of as being associated with flowering plants, Angiospermae, but it is now realized that most extant Cycadaceae (one family of the non-flowering Gymnospermae) seem to be pollinated by insects also. Both groups of plants produce pollen (i.e., microgametophytes of two or three cells) that must move from the microsporangia to the megasporangia, in which fertilization of ovules takes place, followed by embryogenesis, seed development, and fructification. Which insects were the first pollen vectors (i.e., pollinators) is a matter of debate. Both Diptera and Coleoptera have been suggested (reviewed by Labandiera and Bernhardt, respectively). Perhaps there is no reason to assume that the two suggestions are mutually exclusive.

Within Diptera, short-horned flies are noted having tubular mouthparts that fit with feeding at flowers. Coleoptera as early pollinators are thought to have been associated with heavily constructed flowers (such as those of Magnoliaceae, the magnolias) in which they fed on floral tissues (tepals and ovaries) and pollen, spreading pollen between flowers by "mess and soil." Nowadays, Diptera, Coleoptera, Hymenoptera, and Lepidoptera are the most conspicuous and well-known of pollinators and anthophiles (flower visitors that are not necessarily pollinators). These orders and several minor orders associated with anthophily and pollination are discussed below (Taxonomic diversity).

The details of how flowers attract insects are discussed under "Floral advertising." The benefits that anthophiles reap from flowers (pollen, nectar, and other foods, oviposition sites, mates, and comfort) are discussed under "Floral rewards." Flowers and their symbiont insects comprise evolving and functional ecosystems in a complex interplay of mutualisms and competition (community and co-evolutionary ecology) that are becoming recognized, along with biological diversity, as being crucial to conservation.

Taxonomic Diversity

The Hymenoptera are well known as flower visitors and pollinators, primarily because of the bees (Apoidea) (Fig. 82), which are thought to have co-evolved with reproductive structures of plants, especially flowers. They are adept at handling flowers, gathering pollen (mostly as provisions for their brood) and imbibing nectar. Their specialized, plumose body hairs entrap pollen as they move from flower to flower so that they are effective pollen vectors and pollinators. Honeybees and bumblebees are quick students of floral colors, shapes, and complexity and are efficient foragers. Some bees have special relationships with oil-providing, and gum-providing flowers. The closely related Sphecidae are mostly predatory, but like other families of wasps (Pompilidae and Vespidae), often are seen at flowers feeding mostly on floral or extrafloral nectar. The Masaridae (Vespoidea) are almost all vegetarian and are especially associated with anthophily. The ants (Formicidae) also may frequent flowers. There are only a few examples of ant pollination, but their association with flowers and

Pollination and Flower Visitation, Figure 82 **Honeybee, *Apis mellifera*, a common daytime visitor of flowers (photo Andrei Sourakov).**

extra-floral nectaries often protects the flowers and seeds from predation. Most other families in the suborder Apocrita are parasitoids. There are many examples of these kinds of wasps feeding from nectar at flowers. Because they mostly have unspecialized and short mouthparts, they are found mainly on open-bowl shaped flowers with exposed nectar. Indeed, floral nectar may be a crucial resource to fuel their activities, especially as young adults that have not yet found hosts or mates. Among the herbivorous families of Apocrita are the Cynipidae (the gall wasps) and several species of seed-eating and gall-forming Chalcidoidea. Notorious among the chalcidoids are the Agaonidae, the fig wasps, which have tightly co-evolved relationships with *Ficus* species (figs). The wasps oviposit in the enclosed inflorescence (flower). The larvae then mature as the fig inflorescence ripens into a complex infructescence. The newly emerged adult female wasps collect pollen in specialized pouches and seek out new inflorescences in which to lay their eggs. Pollination of the fig inflorescences occurs as a byproduct of the reproductive behavior of the wasp species.

Among the Symphyta (the other suborder of the Hymenoptera which includes the sawflies), anthophily is less well studied. They sometimes are found on flowers, often well dusted with pollen, and feed on nectar. Some species seem to be associated with pollination, especially of orchids in Australia.

The Diptera are highly diverse as flower visitors. Many families of long-horned flies (Nematocera) derive their carbohydrate nutrition from feeding at flowers. This habit is especially well studied in mosquitoes (Culicidae). Males feed on floral nectar for fuel in swarming flight, and females may feed on nectar prior to searching for mates and blood. Some orchids are pollinated by mosquitoes. The idea that blackflies (Simuliidae) are pollinators of blueberries (*Vaccinium* spp.) is not correct, but nectar feeding is known in this group. Nectar feeding and pollination is attributed to most nematocerous families, especially in relation to floral mimicry. Some plant groups, notably Araceae and Aristolochiaceae, attract flies by scents and colors that mimic such fly-attracting substrates as dung, carrion, musk, and fungi. Among the midges (Ceratopoginidae) are a few specialized species that bite open pollen grains to feed. Cacao is pollinated by midges. Among short-horned flies (Brachycera) there are also many flower visiting species. Particularly interesting are the long-tongued Tabanidae (horse flies) and Nemestrinidae (tangle-veined flies) of southern Africa. Some species have highly specialized pollinating relationships with plants in the iris family (Iridaceae). The flower flies, or hover flies (Syrphidae), are probably the best known of the Brachycera for their close associations and pollinating activities with a wide variety of plants. Among the Diptera, the 50 families of acalypterate muscoids are poorly represented as flower visitors, with records associated with only the pomace flies (Drosophilidae) for which yeasts and floral nectars are parts of the symbioses. The calypterate muscoids generally are well known as flower visitors. Their roles as pollinators have been explored in various plants, including the umbels (Apiaceae), and especially the mimetic Araceae, Aristolochiaceae, and Rafflesiaceae.

Almost all Lepidoptera visit flowers and imbibe nectar. The exceptions are those that do not feed as adults (some microlepidoptera) and perhaps some of the specialized moths that feed on animal secretions, and even blood. Some Micropterigidae feed directly on pollen. Also, a few butterflies (for example, *Heliconius*, *Parides*, *Battus*) use pollen as food. They place pollen into floral nectar and make a "pollen soup." They then imbibe the nectar enriched with the eluents of the pollen. Most butterflies and moths have elongated, tubular mouthparts and imbibe nectar that is dilute (less than 45% sugars). One of the longest proboscides is that of *Xanthopan morgani* f. *praedicta* (Sphingidae), the existence of which was predicted on the basis of an orchid from Madagascar, *Angraecum sesquipedale*, with its 25–30 cm nectariferous spur. Some moths (for example, *Plusia gamma*) secrete saliva and dilute heavy nectar at open-bowl shaped flowers.

Moths, particular Sphingidae, hover while feeding at flowers and have high energy demands. The flowers they visit and pollinate tend to be presented with outward facing tubes (like trumpets) and secrete copious nectar. They are also often heavily scented. The nectar of flowers visited by hawkmoths are weak in amino acids. It has been suggested that too much amino acids ingested with large amounts of nectar could be toxic. Many pestiferous moths feed extensively at flowers, but their activities, being nocturnal, are not well understood. The army cutworm moth (*Euxoa auxilliaris*) is migratory from the U.S. plains to the Rocky Mountain alpine ecosystem. In the summer, the moth does not aestivate (become quiescent), but feeds extensively on floral nectar, converting the sugars to fat before return migration and sexual maturation. The resident moths of the same family (Noctuidae) do not show that pattern of activity and reproductive diapause.

Some special relationships have co-evolved between Lepidoptera and flowering plants. One of the best studied is that between *Yucca* spp. (Liliaceae) and its pollinating moths (*Tegeticula*). These moths gather pollen in their mouthparts and carry it between flowers of different plants, stuff the pollen mass into the stigma of the flower, and then lay their eggs in the floral ovary. As the ovary matures, the larvae eat some of the developing seeds. There are other similar, but less well appreciated examples (for example, *Hadena bicruris* and its oviposition behavior on *Silene alba*).

Butterflies are diurnal and less energy demanding than moths in their flower visiting. Many of the flowers with which they are associated have tubular corollas that flare and provide landing platforms for the settling butterflies. The flowers are often brightly colored, sometimes distinctly reddish, and mostly not strongly scented. Butterflies often forage sporadically, visiting flowers that may be widely spaced and not visiting those along the way. Pollination by butterflies has been rarely proven to be important, mostly because specific studies have not been made. For migratory butterflies, especially the monarch (*Danaus plexippus*), considering the importance of nectar corridors is part of conservation efforts.

The Coleoptera is a hugely diverse order and members of about 30 families have been recorded from flowers. Members of the suborder Adephaga (i.e., Caraboidea) are not flower visitors, although a few records have been made. Among the suborder Polyphaga, flower visiting is widespread among the families, but not in any apparently systematic way. Among the Hydrophiloidea and Staphylinoidea, anthophily is recorded only for a few Hydrophilidae (or Hydraenidae) and Staphylinidae and Ptiliidae, respectively. The Scarabaeoidea has anthophiles in the Scarabaeidae, with pollination relationships ascribed to a few species. There are a few records of anthophiles in the Elateroidea (Elateridae), the Buprestoidea (Buprestidae), the Cantharoidea (especially in the Cantharidae, and a few in the Lycidae) and in Dermestoidea (Dermestidae). In the Cleroidea, flower visiting is well represented in the most diverse families (Cleridae, Melyridae). Among the wide array of families in the Cucujoidea is a smattering of anthophilous families (Nitidulidae, Rhizophagidae, Coccinellidae, Lagriidae especially some Scraptiidae, Mordellidae, Oedemeridae, and few Anthicidae). The Chrysomeloidea has anthophily recorded from a few Cerambycidae, Bruchidae, more Chrysomelidae, and many Curculionidae. Only the Melyridae, Mordellidae, and Oedomeridae seem to be exclusively anthophilous, however, the nature of the relationships of those beetles with flowers is mostly unknown.

A wide variety of other taxa use flowers in various ways. Collembola have been recorded from flowers from all over the world. They seem to be mostly pollenophagous, but some feed on nectar. There are a few records of Plecoptera (stoneflies) on flowers. Among the Orthopteroid orders, flower visiting is known, but rarely studied. Some Dictyoptera visit flowers. For example, cockroaches may be found in the inflorescences of palms and may be involved in some pollination in the canopy of tropical forests. Some mantids use flowers as sites from which to ambush prey and some have floral-mimicking coloration. Dermaptera (earwigs) often are found in flowers, but seem to be mostly destructive, feeding on the stamens and pistils. Among the Grylloptera, some long-horn grasshoppers (Tettigoniidae, especially *Conocephalus*) also feed destructively on flowers. The Australian Zaprochilidae have elongated heads and prognathous mouthparts that suggest floral feeding. The Orthoptera proper (short-horned grasshoppers) are not often found in flowers, but some, as nymphs, may feed destructively there.

Various Hemiptera sometimes are encountered feeding in flowers, notably Nabidae, Miridae, Lygaeidae, Coreidae, Pentatomidae, and Phymatidae. Among the phymatids, both nymphal and adult ambush bugs are well known to take prey at flowers. The way they choose which flowers to use seems to reflect ease of movement, alate adults being less choosy than strictly ambulatory nymphs. The importance of various predatory Hemiptera in biocontrol suggests that much more needs to be known about their nutritional needs outside their prey. Among the hemipterans, flower visiting is not well known, but some mimic flowers or inflorescences in group activity (for example, Flattidae).

The thrips (Thysanoptera) often are found in flowers. Some have specialized asymmetrical pairs of mandibles that allow them to crush pollen grains. Thrips can build up huge populations in flowers, and may be pestiferous in the horticultural trade. They are invoked as pollinators in some special situations. In the Malaysian forest trees (Dipterocarpaceae), the development of thrips populations has been associated with multi-specific plant flowering phenology, sexual reproductive strategies (breeding systems), and pollination.

The potential for lacewings (Neuroptera) for biocontrol of pest insects has stimulated research into their flower visiting activities and nutritional needs. It seems that nectar or pollen feeding, or both, is important for their longevity and persistence.

Floral Advertising

Flowers can be considered as advertisements for plant sex. Primarily, they exploit the senses of vision and smell, but at close range and on flowers, taste and touch come into play. Color vision is general in insects. It is like color vision in human beings because, in most species studied, three primary colors are involved (trichromacy) but, unlike in human beings, the primary colors are ultraviolet (UV), blue (B), and green (G) rather than B, G, and red (R). Some insects seem to have tetrachromatic (UV, B, G, R) color vision, while others are deuteranopes (UV, B+G) Most of our understanding of color vision in insects comes from the western honeybee (*Apis mellifera*). The neural coding is also different from our own, so that brightness is not important and the green receptor is involved in other visual tasks as well as resolving colors. Thus, in studies of colors of objects of interest to insects, the whole insect visual spectrum must be considered, not just UV and not just the B and G parts of the spectrum. Many flowers show UV patterns that are invisible to people. In general, more architecturally complex flowers with hidden rewards and sexual organs tend to have color pattern guides (UV or not) more often than simpler, open flowers.

It has been assumed that floral color and size act as long-distance attraction for floral visitors. However, recent research has shown that discs of about 8 cm diameter become visible to honeybees only at a range of less than a meter. Moreover, the colored discs must have color and green contrast with the background to be even that visible. Without green contrast, the distance for detection declines to a few centimeters. The green receptor is involved in the detection of the edges of shapes, movement of objects, shape recognition, and such tasks as landing after flight. Another component of flower form that has been investigated recently is the importance of the dissectedness of the outline. It was assumed that dissectedness of the outline added attractiveness to flowers, but circular targets are detected over longer distances than those of the same diameter with variously dissected outlines.

Flowers produce a wide variety of scents. Some are mimetic, as noted above under Diptera and Coleoptera as flower visitors and pollinators. "Heavy" floral scents are associated with flowers that bloom and are pollinated at night, mostly by moths. Those scents are assumed to attract pollinators over long distances, and the highly developed olfactory sense of the moths is well known. Diurnally blooming flowers tend to have more delicate "floral" scents. These seem to be used by floral visitors at close range. Different parts of flowers emit different smells that are used in orientation. Once the visitor has landed, the definition of scent and taste becomes blurred, as antennation allows the visitors to follow odor/taste guides on the surface of the floral parts.

Coupled to the subtleties of floral size, shape, color, color patterns, scent, and odor/taste guides may be the role of micro-textural features of the floral epidermis. Insects, at least bees, have been shown to use and to learn "micro-Braille" while foraging. The features on the floral surface match the scale of antennal sensilla in size and spacing.

Floral Rewards

Pollen is probably the most important of floral food rewards for anthophiles, but may have been coupled with sugary drinks (nectar) since the association of spores and micropylar droplets in the Carboniferous. Pollen of entomophilous (insect-pollinated) plants is generally highly nutritious. Depending on the plant species of origin, it contains variable amounts of protein (even up to about 60%), many amino acids (including those essential for animal nutrition), lipids (up to about 20%), starch (up to 22%) and most minor, but important, nutrients such as vitamins, sterols, and minerals. Entomophilous pollen is also characterized often by external ornamentation (spines in Asteraceae, Cucurbitaceae, Malvaceae, Cactaceae; tubercules and ridges) and by having an external, oily pollenkitt. Both features enhance adherence to the bodies of pollinating insects for dispersal. Pollen is ingested whole by most insects, and the nutritive protoplast is digested by enzymes that diffuse in so the nutrients diffuse out into the gut lumen. There are some insects that chew or bite pollen grains to extract the nutrition, among them *Atrichopogon* (Diptera: Ceratopogonidae), various thrips (Thysanoptera), some beetles, and Collembola. Pollen ingestion by some Diptera and Coleoptera is associated with maturation of their sexual organs, especially of the ovaries and ova in females. During nesting by bees, pollen is gathered by females and stored as "bee bread" or larval food. The females in most families have specialized pollen collecting (parts of the legs) and carrying organs (scopae, corbiculae). Most female solitary bees lay their eggs on a loaf of bee bread within the cells of the nests.

Nectar is a sugary liquid secreted by various parts of plants, including flowers. Floral nectar is comparatively well studied and is the primary fuel for flight in many insects. The energy content (5 cal/mg of sugar) of nectar depends on the volume produced and its sugar concentration. The concentration of sugars reflects the capacities of various insects to imbibe liquids of different viscosities. The nectar imbibed by long-tongued insects such as Lepidoptera, some Diptera (e.g., Nemestrinidae, some Tabanidae, Bombyliidae), and some Apoidea (Bombinae, Euglossinae) is usually watery (around 30% sugars), whereas that taken by short-tongued and lapping insects (e.g., Muscidae) may even be crystalline. The main sugars (sucrose (a disaccharide), glucose, and fructose (monosaccharides)) vary with plant family and type of pollinator. Some generalizations can be made about pollinator type and the ratio of sucrose to fructose and glucose in nectar. If this ratio is high, pollination by insects with short proboscides (Diptera, short-tongued bees) is expected; if it is low, pollination by insects with long proboscides (Lepidoptera, long-tongued bees) is expected. Floral nectar contains minor constituents, among which amino acids are the best understood. Floral nectars consumed by insects (e.g., many Diptera, bees) with nitrogen-rich diets tend to have lower titers of amino acids than do those consumed by insects that do not feed on nitrogen-rich diets (e.g., most Lepidoptera, long-tongued Diptera). The role of amino acids in nectar in the nutrition of anthophiles has been investigated rarely, but it is known that some insects have greater longevity when allowed to feed on nectar rather than on syrup of the same sugar concentration. Little is known of the other minor constituents, save their presence. Lipids often are accompanied by antioxidants (for example, ascorbic acid) and may be involved in reducing evaporation rates of water from exposed nectars.

Among the Apoidea (especially *Centris* species in the subfamily Anthophorinae) are specialists that collect floral oils from the flowers of certain families of plants, such as Malpighiaceae and Krameriaceae. These bees use the oils for provisioning their nests and collect it on specialized tarsal brushes. Many bees collect resins and gums, but some flowers provide it as a reward for their pollinators. *Dalechampia* species and *Clusia* species are well-known provenders of gums that the bees use in nest construction. Among the Euglossinae (Apidae) are species in which male bees collect floral scents, especially of orchids, that they use as olfactory attractants for mates in lekking behavior.

Other Floral Rewards: Heat, Floral Tissue, Sex

Some blossoms become heated. Among the mimetic Araceae, such as jack-in-the-pulpit and skunk cabbage, endogenous heat production is well known. The pollinators of these plants are various flies and beetles that become temporarily trapped in female phase blossoms that become male as the stigmas senesce and anthers shed pollen, which is when the pollinators are liberated. The heat helps drive off the mimetic scents (dung, carrion, musk), speed floral and insect development, and bring the pollinator sexes together for mating. Other flowers trap the heat of the sun by various means. Parabolic diaheliotropic (sun-following) flowers may warm their insect visitors by six or more degrees Celsius. Such heating improves speed of mobility, and, it seems, optical and other neural processing. Catkins of willows (*Salix* spp.) act as hairy heat traps and offer shelter and warmth to small insects, such as non-biting midges (Chironomidae) in the Arctic. Some insects, especially male bees, sleep in flowers. The males of the hoary squash bee (*Peponapis pruinosa*: Anthophorinae) sleep, often in small bachelor parties, in the spent flowers of squash and pumpkin (*Cucurbita* spp.) that open and close in a single day.

A wide variety of insects feed on floral tissues, apart from pollen. Many, for example, caterpillars, maggots, earwigs, thrips, and some beetles, probably are not pollinators, but some are. Notorious are the highly mutualistic interactions between figs and fig-wasps, yucca and yucca-moths, globeflowers and the anthomyiid flies, oil palms and its pollinating weevils, and some special fly-pollinated flowers (for example, *Siparuna* species (Monimiaceae)). The flowers, mostly the female parts and resulting fruit (except in oil palm and *Siparuna*), serve as oviposition sites and for brood food. The adult insects are the pollinators. Some thrips breed in flowers, becoming serious horticultural pests in some situations. Other sorts of floral tissues seem to be fed on by some anthophiles and pollinators. Special structures, food bodies and staminodes with pollen substitute (for example, in Melastomataceae) are eaten or collected by various insects, including bees.

There are a few flower visiting arthropods that use flowers as sites for prey capture. Well known are some species of crab spider (for example, *Misumena* species (Thomisidae)) and ambush bugs (*Phymata* species (Reduviidae)). These predators choose their ambush sites according to energetic constraints of changing site. For example, adult female crab spiders that walk slowly from place to place are most careful in choice, immature and apterous bugs are also fastidious, but adult alate ambush bugs choose quickly and switch sites readily. Some tropical mantids are cryptically colored to match the flowers they use. Some crab spiders may be able to change color to match their floral host.

Flowers may be mating sites for some insects, as recorded for a few species of bees. Some insects, such as the males of some orchid bees (*Euglossa* spp. (Euglossini)) and some flies collect floral scents that become attractive to mates.

Energetics: Time and Motion

A great deal has been learned about optimal foraging from insect and flower relations. Bees, especially bumblebees (*Bombus* spp.), are central place foragers (i.e., they forage from a home, the nest), are conspicuous and quite easily followed. Their foraging illustrates the range of behaviors that exemplify maximizing energy gathering while minimizing energy expenditure. Foraging bumblebees tend to follow the same general path from one trip to the next. Thus, they are familiar with their area. They also tend to visit the same patches of flowers on sequential trips, a behavior sometimes called "trap-lining." Within a patch, bumblebees usually show a "forwarding" path, but this may involve sharp turns to left or right and visiting mostly "next-closest" blooms if resources present are relatively abundant and rich. If resources are sparse, the bees tend to veer back and forth much less between sequentially visited blooms, and often overfly the "next closest." Thus, in a rich patch they visit more and stay longer, but in a poor patch, they sample and depart quickly. On the blooming plants, the bees tend to act systematically. For example, on tall inflorescences, they start at the lowermost open flowers and work upwards. The energetic implications are for efficiency, crawling vertically instead of flying, and flying down between adjacent inflorescences. Mostly, such inflorescences have female-phase older flowers and male-phase younger flowers (protandrous flowers), with more dilute nectar below and less, but sweeter, above. Most of the studies that exemplify those movement patterns have been made in meadow-like situations. On trees, with vertically arranged arrays of blooms, the same within-patch pattern has been noted. However bees treat inflorescences close to each other as a unit and continue upward but they treat separated (more than 10 cm apart) inflorescences as individuals and so show a generally descending overall direction. The implications for pollination of trees remains to be explored.

Flowers are variable in their anatomical complexity. Thus, simple, open-bowl-shaped flowers are easily exploited, but complex flowers with intricate mechanisms and hidden rewards require skill on the part of the pollinators to use. Experiments with bumblebees have shown that learning to manipulate complex flowers with skill, accuracy, and speed requires learning and an investment of time. That investment can pay off through the much greater amounts of reward in complex flowers versus simple ones. Of course, if too many bees invest in the learning when there are few flowers, loss in profitability from investing in learning may result.

The models of optimal foraging by bumblebees can be extrapolated to predator and prey interactions, but blossoms do not try to escape (quite the contrary, they advertise their presence), worker bees forage for the colony rather than for themselves, and their demise as individuals is not as drastic a loss for the next generation as in non-eusocial animals. Nevertheless, in such flower-visiting animals as sphinx moths and hummingbirds, the similarities in foraging patterns are remarkable. Butterflies tend to forage in a much more haphazard fashion, sipping nectar at flowers as they need energy (Fig. 83).

Floral specialization and constancy in the broad sense include the tight interspecific interactions between specialized pollinators and their partner flowering plants (for example, *Yucca* and *Tegeticula* (Lepidoptera), *Ficus* and *Agaonidae* (Hymenoptera), oil palm and *Elaeidobius* spp. (Coleoptera), *Siparuna* and Mycetophilidae (Diptera), and the myriad bees and flower specializations. The terms mono-, oligo-, and polylectic (or -tropic) refer to anthophiles that use one, a few, and many

Pollination and Flower Visitation, Figure 83 Moths such as this sphinx moth visit flowers at dusk or during the evening (photo R. J. Barnas).

floral resources. The equivalent botanical terms for flowers are mono-, oligo-, and polyphilic. Entomologists and naturalists have made observations of apparent, but unexplained, floral specializations in other groups of insects in which generalist anthophily might be otherwise expected (e.g., in Syrphidae (Diptera), other Diptera, and some Coleoptera). Apparent floral "specialization" (mono- or oligolecty) may be thrust upon anthophiles by lack of a diversity of flowers upon which to forage. Presented with more kinds of flowers, such anthophiles would presumably expand their foraging base. Constancy is a term best reserved for oligo- or polyleges that restrict their visits to the flowers of one species of plant, even when others are in bloom. Such constancy is well explored by studies of social bees (Apidae) in which individuals from a single colony may be constant to the flowers of a particular plant for a short period before switching to another, while other individuals from the same colony may be constant to yet a different species, and so on. The benefits of constancy are clear from the viewpoint of intraspecific pollination, and from the anthophile's viewpoint, in efficiency of learning to forage quickly and accurately. Such foragers, either as colonies as in honeybees, or as individuals, have species of plants that can be called "majors" and "minors" so that they sample the floral resources in their areas and can switch as resource availability, type or quality change in the habitat or according to the colonies' needs (Fig. 84).

Pollination and Flower Visitation, Figure 84 Scanning electron micrograph of pollen of the oil palm (*Elaeis guineesis*) on the snout and compound eye of a weevil, *Elaeidobius kamerunicus*, the major pollinator of oil palm.

Ecosystems, Community and Co- Evolutionary Ecology

Various ecosystems and communities have particular assemblages of plants and pollinators, for example, the Arctic, New Zealand, and alpine communities with pollination predominantly by flies. In general, there appears to be a positive relation between phytosociological progression (by succession, habitat, or geographic area, or combinations thereof) and specialization and diversity in pollination mechanisms. How those various diversities of pollination partnerships came about evolutionarily may be outlined as follows. Starting with the idea that flowers may sometimes compete for pollinator services and sometimes pollinators may compete for floral resources, it can be invoked that some individuals and some species fare better than others. If the direction of competition remains the same over a period of time, one would expect some evolutionary changes to take place in some of the partners. These changes would involve directional selection and character displacement to result in better adaptedness in species of any group, or of groups of species comprising the partnerships. Thus, the assemblage of flowers and pollinators might change in species abundances and diversities as generalists become more specialized through pressures of resource partitioning (increased reliability of pollination for the plants by specialist pollinators, and lesser interspecific competition for floral resources for the pollinators). The direction of competition probably naturally fluctuates over the short term (years to centuries), but with long-term (thousands to millions of years) trends. It is presumably through those processes, and their reversals, that the complexity of pollination, and other ecosystem functions, has arisen. The extreme situation of the evolution of eusocial pollinators (which are found everywhere from tropical forests to high arctic tundra and exhibit constancy and specialization) has depended on a flora of plants with short-lived flowers (from open-bowl shaped ones visited by a wide diversity of pollinators to specialized ones that only the eusocial pollinators can service) blooming in sequence throughout the long life-span of the insect colony. Co-evolution in pollination is a complex process.

Pollination for Food and Fiber Production

Although many agricultural crops are independent of insects for pollination (wind pollination in grains, self-pollination in some seed crops and vegetables), others require insect pollination. Honeybees (*Apis mellifera* and *A. cerana*) are especially important, and stingless bees (Meliponini) are gaining recognition also. The importance of leafcutting bees (especially *Megachile rotundata*) in agriculture came to prominence for production of alfalfa seed and the culture of these bees is now a multi-million dollar industry. In Japan especially, but also in other places, mason or orchard bees (*Osmia* spp. (Megachilidae)) are managed as pollinators for use in fruit production. Bumblebees (*Bombus* spp. (Apidae)) are now firmly entrenched as part of technology for greenhouse production, especially of tomatoes, around the world. Flies (especially Calliphoridae) are used in pollination of some crops (for example, seed production for onions, carrots, parsnips), and are probably the principal pollinators of mango. Midges (Ceratopogonidae) are the principal pollinators of cacao. Rotting vegetation is used in plantations to provide oviposition sites and food for the maggots to assure adequate pollinator forces for the crop. Some beetles (Nitidulidae) are the principal pollinators of Annonaceae. In these, and other crops for which even less is known, much research is needed to determine how to provide the pollination forces needed from crop production.

The importance of pollinators to forest sustainability has been hardly investigated, but it seems reasonable to suggest, from evidence in Costa Rica, Thailand, and Canada (Ontario, Quebec, New Brunswick) that pollination has been adversely affected by human activities (logging, pesticide applications, fragmentation). Grasslands in South Africa and Canada also seem to be suffering declines in pollinators and pollination through overgrazing.

As mentioned, honeybees (*Apis* spp.) are especially important pollinators in agriculture throughout the world, and where they are native, are part of the natural ecosystem. Beekeeping has come to grips with the issues of pesticide kills, but recently in Europe and North America, has suffered major setbacks with the spread of exotic diseases. Varroa mites transmitted from the natural host, the Asiatic hive bee *Apis cerana*, onto the western honeybee, *A. mellifera*, continue to adversely impact natural, feral, and managed colonies. Conversely, diseases of the western honeybee have been transmitted to Asiatic species. In some places now, honeybees are in too short supply to service growers' needs. Moreover, as beekeeping has come to require more intensive management to maintain healthy, strong colonies, the costs of pollination services have risen. In some places, notably in China and parts of Nepal, bees are so scarce that apple pollination is now done by hand.

The economic impact of pollinator shortages are crops failing to reach potential yield levels locally, regionally, nationally, or globally. The effects, depending on scale, may be rising prices or farmers being unable to produce with profit. Whatever the effect, prices to consumers rise. The needs for pollinator conservation are clear.

Insect Conservation

There are relatively few insects on lists of rare and endangered life forms by comparison with birds, mammals, and plants. Most insects on such lists are butterflies. Flower relations and pollination are central to conservation because rare and endangered flowering plants must have their mutualists with them in their habitats if the populations are to persist. Thus, pollinators and seed dispersers must be included in conservation and restoration planning. That approach is being embraced in Hawaii for plant conservation, especially for endangered bird-pollinated plants. Also in the Carolinian forest fragments of southern Ontario, sensitivity to the need for pollinators in rare plant conservation is recognized. Several magnificent trees, for example, cucumber magnolia, Kentucky coffee tree, and the native paw, fail to set fruit for various reasons such as pollinator limitation and wide spacing of trees.

The vicious cycle involving the demise of pollination mutualisms and the partners of those mutualisms proceeds as follows. The general habitat is stressed (by fragmentation, pollution, etc.) so that one or more components become scarce. If one of the dwindling components is part of a crucial mutualism, such as pollination or seed dispersal, then the partner not directly affected by the stress becomes indirectly affected and dwindles too. As the community become simplified by erosion of diversity and abundance, other components become adversely affected. So the system, as a whole, can be seen to become less and less diverse in terms of species present and the interactions that make for a functioning ecosystem. The complex is simplified, and a different ecosystem becomes established.

There is now global concern for the demise of pollination in agricultural and forest ecosystems. In agriculture, pollination services are variously threatened by adversity, disease, and pests in beekeeping (for example, fluctuating honey prices, mite and other diseases, small hive beetle); pesticide poisonings of pollinators; expansive cultural practices that remove pollinator habitat from proximity to crops (for example, as happened by expanded alfalfa seed production fields in the Canadian prairies in the 1940s and 1950s); and reduction in the amount of natural or semi-natural areas in agricultural regions. In forestry, large scale clear-cutting, especially now in the tropics (the effects in much of the temperate world are now largely unrecorded history), seems to be adversely affecting populations of various flower visiting insects. Some insects, notably generalist bees, seem to have a remarkable propensity for persistence, but many specialists do not have that capacity.

Pollination deficits in agriculture are documented in various parts of the world and have become common enough to prompt major international concern, especially for sustainable food and fiber production for human life. The International Convention on Biological Diversity acted over 1998–2002 through the International Pollinators Initiative of the Food and Agriculture Organization of the United Nations. Various other national and continental programs also have started (for example, the World Conservation Union, and various regional initiatives such as the North American Pollination Protection Campaign and the African Pollinators Initiative).

► Pollination by Yucca Moths
► Night Blooming Plants and Their Insect Pollinators
► Bees
► Honey Bee
► Alfalfa Leafcutting Bee
► Apiculture
► Plant Extrafloral Nectaries

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Pollination by *Osmia* Bees (Hymenoptera: Megachilidae)

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Most of the plants of agricultural value are angiosperms, plants characterized by the presence of flowers with ovaries formed by one or more carpels. The flowers are normally hermaphroditic, having both male and female reproductive organs, but there are also plants with unisexual flowers. The reproductive organs of insect-pollinated plants correspond to the morphological and behavioral characteristics of the pollinators, and result from the co-evolution of the plant and pollinator.

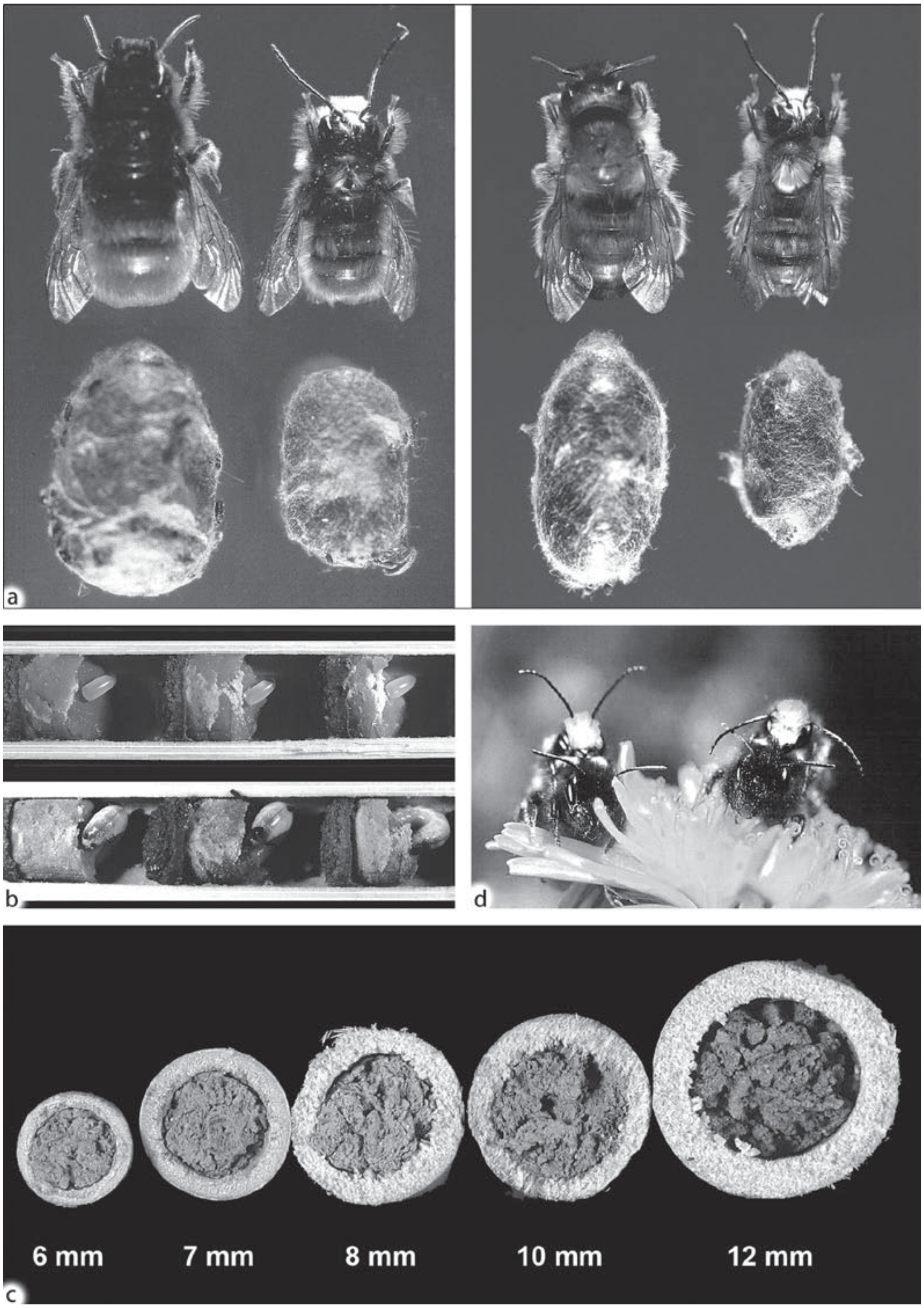
In an hermaphroditic flower, the male organ is represented by one or more stamens, each formed by a filament terminating in an anther in which pollen grains are formed. The female apparatus is formed by one or more carpels joined together in various ways to form the ovary containing immature seeds, and from which a slender column, or style, arises and culminates in an expanded tip or stigma.

There are two phases in the reproductive process, pollination and fertilization. Pollination is the transport of pollen from the stamen (anther) to the stigma; fertilization is the fusion of the two germinal cells and all the biochemical exchanges that follow. Once on the stigma, the pollen granule is held by the papillae, which cover the surface, and possibly by exudates. When the pollen granule comes in contact with the stigma it germinates; it then develops and forms the pollen tube, which grows through the style, reaching and fertilizing the ovule. There are numerous agents responsible for pollination: wind, water, insects and some vertebrates.

Many crops of agricultural interest are mainly insect-pollinated, so the work of pollinating insects is often necessary or at least useful for a bountiful harvest. Among the pollinating insects, bees are most widely employed to obtain pollination service. The transport of pollen from flower to flower occurs during a short period of blossoming, so it is imperative that these pollinators be active at the correct time.

Many wild bees are favored by warm weather, even though different species vary in their temperature optima. *Osmia* species (Fig. 85), depending on the species, are active from February (*Osmia cornuta*) to September (*Osmia caerulescen*) and they can forage under cool and cloudy weather. They are found in all kinds of environments, though they prefer open, sunny habitats and a variety of flora. Almost all *Osmia* species are gentle, not aggressive, and have a brief nesting period. These characteristics are associated with the ease at which *Osmia* can be induced to nest in artificial nests. This, and their strong gregarious nesting tendencies, are the base for the management and multiplication of these insects for crop pollination.

The use of *Osmia* for pollination of orchards was first attempted during the second half of the last century in Japan with the species *Osmia cornifrons*. From the very beginning, satisfactory results were obtained in using these species as orchard pollinators, and the practice has been continued and advanced to the present day. Today



Pollination by *Osmia* Bees (Hymenoptera: Megachilidae), Figure 85 *Osmia* bees: (a) *Osmia cornuta* Latr., female and male with cocoons (left) and *Osmia rufa* L. female and male with cocoons (right). (b) *Osmia cornuta* Latr. newly laid eggs (above) and larvae (below). (c) Cane (*Arundo donax* L.) segments of suitable diameter for the nesting of *Osmia rufa* (6–8 mm) and *Osmia cornuta* (8–12 mm). Mud seals are visible. (d) *Osmia cornuta* Latr. mating on a *Taraxacum officinalis* flower.

the majority of apple orchards in Japan are pollinated with the aid of *Osmia*.

During the 1970s and 1980s, investigators in the USA started investigating the native American species *Osmia lignaria* as a pollinator of orchards, then somewhat later began examining the possibility of using a species introduced from Japan (*O. cornifrons*) for this purpose. At the same time, investigations were initiated on the possibility of using *Osmia rufa* as pollinators in Denmark and England, and *Osmia cornuta* in Spain, Serbia, and Italy. The technology of raising *O. cornuta* is well known, and this bee can be reared in the desired numbers.

The use of these bees for field pollination cultivations has been very successful, especially for early-flowering fruit trees. Good results have also been obtained recently for pollination of crops grown in confined environments.

Osmia Biology

Osmia bees are found in the order Hymenoptera, suborder Apocrita, superfamily Apoidea, and family Megachilidae. The genus *Osmia* Panzer consists of 213 species. They are spread over the old and new world in the Palearctic, Nearctic and Ethiopian regions, but are not found in the Indo-Australian and Neotropical regions. In most cases, *Osmia* spp. show a well-defined sexual dimorphism and an obligatory univoltine type of life cycle. They spend the winter in their cocoons as diapausing, fully-formed adults. Each cocoon is found inside a pedotrophic cell (each cell contains an egg and stored food in a suitable amount for the newly hatched larva). Often the cells are placed in a series of rows inside the nests. The latter are sometimes made in wall cavities, old snail shells, old nests of other insects, hollow canes or stems of plants (Fig. 85). *Osmia* nests have also been found in electric outlet holes and in other kinds of cavities. However, nesting always occurs in pre-existing cavities and usually with well-ordered rows of cells. Nesting females use cavities without contributing to building them. In some cases, as for example with *Osmia coerulescens*, nesting does not consist of ordered rows of cells.

In spring, generally between February and July, according to the species, adults emerge from the cocoon. The emergence of the adults is protandrous; males tend to emerge about a week earlier than the females. When females emerge, mating occurs. Mating can occur on a flower, on the ground, or close to the nest, but never in flight.

Field Pollination

Because the bees collect pollen and nectar from flowers that are near their nests, and they generally will not fly more than 100 m away from the nest, good pollination is achieved by placing nests and cocoons in the orchard with spacing of about 20–50 m. A good rule for open field pollination is to build a shelter in the middle of the field and place a large number of artificial nests inside, together with aerated dark boxes containing cocoons with insects ready to emerge. These containers must be kept away from direct sunlight or the insect-containing cocoons will generate high concentrations of CO_2, which quickly causes high mortality. Furthermore, in order to avoid the dispersal of females that are seeking nesting locations, it is desirable to put artificial nests in the field, thereby retaining the females. Good results have been obtained by distributing ten artificial nests, each containing a hundred tunnels, per hectare.

As a general rule, two to five females per fruit tree in blossom is sufficient to achieve 50–90% of pollination, depending on the orchard. A single hectare of apple or pear trees requires 350–500 nesting females of *O. cornuta*, 500–600 *O. cornifrons*, and 600–1,800 *O. lignaria*, and 1,000 *O. rufa*.

Pear

Most varieties of cultivated pear are self-incompatible, and although self-pollination occurs in some cultivars, fruit-set generally benefits from cross-pollination. Pear flowers usually produce small amounts of nectar with low sugar concentration, so they are not very attractive to honey bees. Honey bees visiting pear blossoms often switch to other, more rewarding plants, resulting in insufficient pollination and poor yields. Moreover, seed-set is important in commercial pear production, and seed number increases with insect pollination. Pears with large numbers of seed are larger and have better shape and flavor than those with small numbers of seeds. Unlike the case with honey bees, *O. cornuta* readily visit pear flowers to collect pollen, despite the low nectar content and quality. Most of the pollen provisions in their cells contain 100% pear pollen, and pollination effectiveness of *O. cornuta* on pear is very high. Thus, *O. cornuta* is a suitable pollinator for pear flowers. *Osmia cornuta* stocking rates for adequate pear pollination have been estimated to be very similar to those estimated for apple (500 nesting females per hectare).

Apricot

This tree blossoms when there are still great differences in temperature, and with frequent frost at night. Many varieties of this plant are self-pollinating, but cross-pollination also occurs. The use of *Osmia* bees on apricot trees can be extremely profitable for the following reasons: *Osmia* bees fly at 10–13°C and tolerate night temperatures below zero; and during this period there are very few competing flowers. The activity of a hundred females per hectare is sufficient to increase fruit set by 30–50%. The same results occur with respect to almond, pear and apple trees.

Chinese-Japanese Plum Cv "Angeleno"

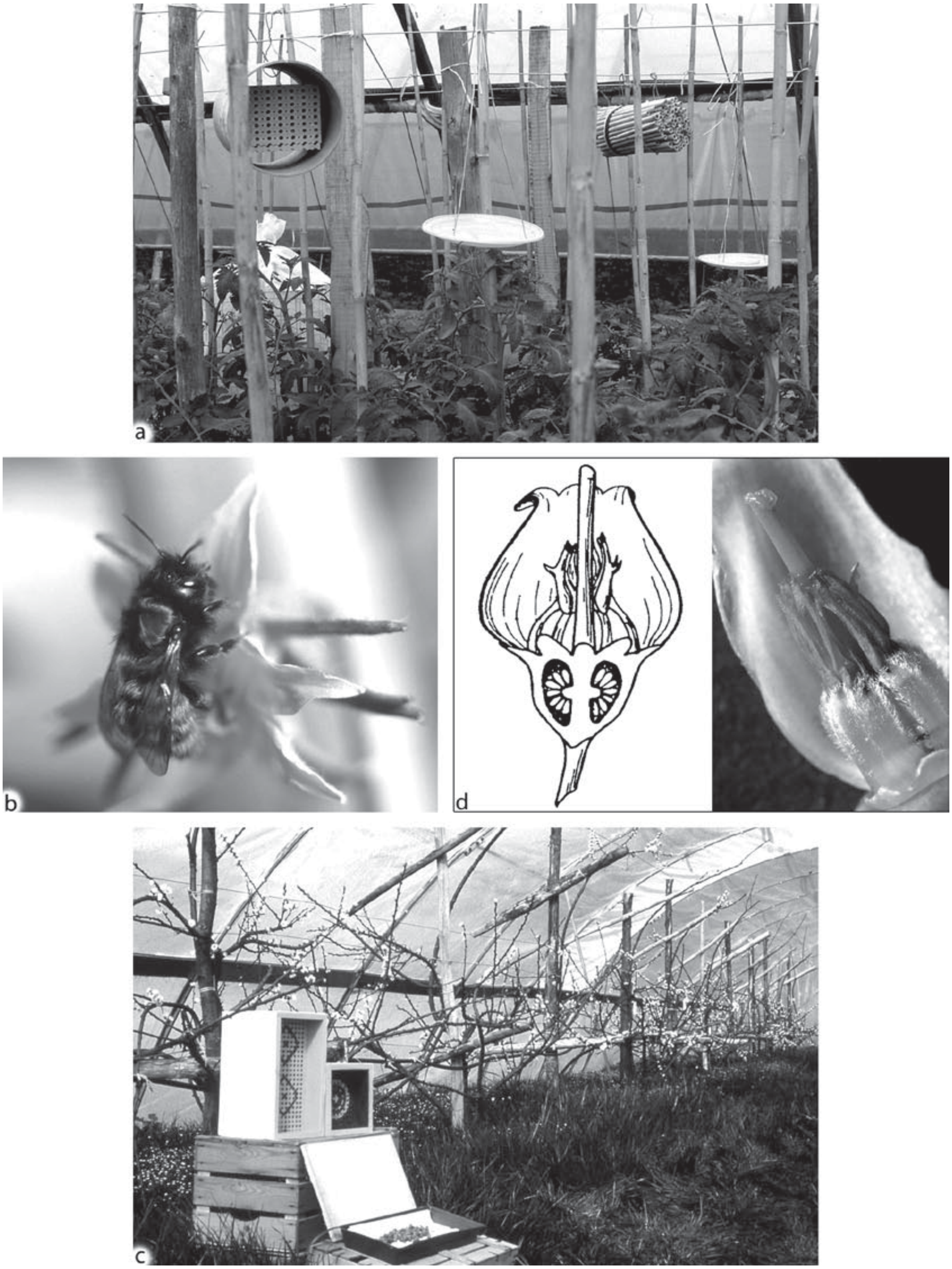
Depending on latitude, the cultivation of this plant has two major difficulties due to limited self-pollination and low nectar production, causing these plants to be unattractive to most pollinating insects. However, *O. cornuta* and *O. rufa* are good pollinators for these plants because they are more attracted by pollen than by nectar, like honey bees and bumble bees. They gather great quantities of pollen as a food reserve for the nest, and gain enough nectar to produce the metabolic energy for flight. For flight they need relatively little sugar, though the presence of flowers is very useful. The reward for the pollination service is therefore mostly pollen, which the *Osmia* gather up in great quantities with the hairs of the ventral part of their abdomen and carry back to their nest. A hundred or so females per hectare are sufficient to obtain an optimal percentage of fruit setting.

Oil-Rape

This crop is very attractive to bees due to the large amount of nectar and pollen. Megachilid bees pollinate this plant with an efficiency comparable to that of honey bees. This crop is a good food source because a large amount of pollen is associated with extensive blossom production, so that the flying and nesting activities can persist for at least one month. With this crop, *Osmia* population densities can increase five-fold.

Cultivation in Greenhouses

Recently it has been shown that *Osmia* are well adapted for pollination in greenhouses, though they do not reproduce well in these structures. Structures containing *Osmia* as pollinators must have side netting or other mechanisms to prevent the bees from escaping. Furthermore, it is very important that structural poles have no holes opening into the greenhouse as these bees are attracted to such openings and tend to get caught and perish inside. *Osmia* are good pollinators for horticultural crops, and extremely positive results have been obtained in the cultivation of tomato (Fig. 86) , pepper and of small fruits such as strawberry, blackberry and raspberry.



Pollination by *Osmia* Bees (Hymenoptera: Megachilidae), Figure 86 More pollination: (a) Cultivation of tomato in a greenhouse; two types of artificial nest traps and an artificial nectar flower are visible. (b) *Osmia cornuta* female on a tomato flower. (c) A shelter with artificial nests near a planting of apricot trees. (d) Flowers of the genus *Vaccinium*: drawing of a *Vaccinium ashei* flower – the stigma edge is over the corolla (left); *Vaccinium corymbosum* flower – the stigma edge is inside the corolla (right)

As in the use of these bees in the open field, in the greenhouse the cocoons must be placed in aerated containers away from direct sunlight. In the case of tomato pollination, because the tomato flower has no nectar for food, it is necessary to place "artificial flowers" inside the greenhouse. These can be made with yellow plastic picnic plates containing sugar-water solution, and they may be hung from the ceiling of the greenhouse. *Osmia* learn easily and quickly include the artificial flowers in their foraging flights to obtain glucose for their own metabolic needs.

Five artificial nests each containing about 50 tunnels and 300 females are necessary for a surface of about 1,500 m^2. To accommodate variation in flowering of tomato plants, it is useful to plan the release of *Osmia* in groups of 30–40 females at a time, in successive intervals of at least 5 days, to be sure of continuing flower pollination. Alternatively, it can be helpful to cultivate tomato plants in conjunction with other nectar-producing horticultural plants such as zucchini, melon, pepper or with *Facelia* sp. flowers.

Considerable financial economy is obtained using bees for pollination. This results from lower manpower costs, and the lack of need for wind generators and mechanical vibrators to facilitate pollination. Also, bees provide better fruit and berry set, and in the case of tomato, they avoid problems with parthenocarpic fruit obtained with phytoregulators. Pollination is especially useful for small fruit production because the flowers have abundant nectar and are generally very attractive to bees.

Blackberry, Strawberry and Raspberry

The flowers of these plants have abundant nectar and are generally very attractive to bees. *Osmia* pollination (Fig. 87) benefits these crops in three principal ways. The first is the increase in fruit size due to better pollination. The second is more uniform fruit due to more uniform fertilization of the drupes (or in the case of the strawberry, achenes). The third important benefit is the reduction of the number of treatments against *Botrytis cinerea*. For example, in the case of raspberry cultivation the treatments are reduced from six to one. The explanation of this phenomenon is the decrease of the nectar volume due to the foraging activity of the bees. In the greenhouse environment, excess nectar stagnates and becomes sticky, thus often causing the sticking together of the sepals and the small drupes and creating a suitable substrate for *Botrytis cinerea*.

Blueberry

Research on pollination of the American giant blueberry (*Vaccinium corymbosum*) by *O. cornuta* in confined environments showed that this bee did not have the pollination efficiency of honeybees and bumblebees. This result is in contrast with the pollination of the blueberry *Vaccinium ashei* using *Osmia ribifloris* in open field conditions. This bee showed a higher efficiency in pollinating blueberry flowers than did the honeybee. It is quite interesting that the morphology of the flower is different in the two species. The *V. ashei* shows the stigma coming out from the corolla while the *V. corymbosum* has the stigma inside the corolla. The *Osmia* bees gather pollen directly with the ventral brush so it is quite difficult for them to collect pollen from the *Vaccinium* sp. that have a very small and deep corolla. So pollination occurs only during nectar sucking visits, and flowers with exposed stigma gain more from *Osmia* visits than those with internal stigma.

Seed and Red Cabbage

Research with *O. cornuta* demonstrated that both these plants are effectively pollinated by the bee in a confined environment. Also, seed yield was double of that obtained with honeybees. These plants are also good candidates for *Osmia* rearing because the population increases

Pollination by *Osmia* Bees (Hymenoptera: Megachilidae), Figure 87 ***Osmia*** **pollination: (a)** ***Osmia cornuta*** **Latr. female collecting nectar from a flower (left); an** ***Osmia*** **female on its back showing the collected pollen (right). (b) Nesting shelter in a plum orchard (left); assembled artificial nest trap in a field of Chinese-Japanese plum, variety Angeleno (right).**

three to five times in confined environments with these plants.

Lucerne and White Clover

O. cornuta and *O. rufa* in a density of 0.50 females/m^2 have been used for pollination of both lucerne and white clover breeding material grown in mesh cages (10 m^2) in summer. For lucerne pollination, *O. cornuta* produce a yield of 8.1 kg/ha while *O. rufa* give a yield of 5.3 kg/ha. Similar results have been obtained for white clover. Both species did not reach the efficiency of *Megachile rotundata* (250 kg/ha), probably due to the high summer temperatures. However, *O. cornuta* show a great efficiency (175 kg/ha) in pollinating off-season in white clover grown in a growth cabinet during winter (24°C/18°C day/night and 16 h photoperiod) if used in a density of 5 females/m^2.

Inhibition of Pollen Germination

For several reasons, bees differ in their pollination capability. One important factor favoring *Osmia* bees relates to inhibition of pollen germination by the bees. *Osmia* gather pollen from the flower anthers without manipulating them. After visiting several flowers, the female bee returns to her nest to discharge the pollen. Pollen gathered by these bees remains viable until the bee discharges it into her nest. In contrast, honeybees and bumblebees quickly inhibit the germination of the gathered pollen. They immediately store the collected pollen in structures called curbicula as they gather it, and this process inhibits germination of pollen. For example, when pollen is compared from anthers and from curbicula, germination rates are reduced 50% in the latter case. Thus, *Osmia* bees are quite effective pollinators.

This is not to say that *Osmia* do not affect pollen. When depositing the pollen in her nest, the *Osmia* female presses the newly gathered pollen on the pollen provision with her clypeus. Extracts of the heads, possibly secretions of the mandibular glands, have been shown to inhibit pollen germination by 75%. The nature of the inhibitor is not known.

► Bees
► Honey Bee
► Pollination and Flower Visitation

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Pollination by Yucca Moths

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Yucca moths provide one of the best understood examples of obligate pollination mutualism, in which the female adult pollinates the flowers of her host plant and her larval progeny consume some of the developing seeds. The yucca moth and its relationship with the yuccas was first described from Missouri in 1872 by Charles V. Riley. At least 25 species of *Tegeticula* and *Parategeticula* (Lepidoptera: Prodoxidae) serve as the exclusive pollinators of an estimated 30–40 species of yucca (*Yucca* and *Hesperoyucca*, Agavaceae). Yuccas have white, usually fragrant flowers in a large panicle, but have effectively lost nectar production and produce very little pollen, thus, they only attract a limited range of floral visitors. A modified urn-shaped stigma of the floral ovary makes pollination unlikely by casual brushing, and only the moths have been documented to be pollinators. The plants can reproduce vegetatively, but the moths appear to be critical for sexual propagation. Geographically limited to the Americas, the moths and yuccas are distributed from southwestern Canada southward at least to northern Belize, with the highest species diversity in arid and semiarid portions of western North America. Over the past two centuries, contiguous yucca range expansion through horticulture in the interior of eastern North America led to rapid colonization by the moths. Within decades, they spread northward to southeastern Canada and westward to the edge of the Great Plains (Fig. 88).

Early studies held that four yucca moth species, including one thought to feed on all but two

Pollination by Yucca Moths, Figure 88 Yucca moth pollinating a yucca flower.

yuccas, served as pollinators of all yuccas. Recent studies based on behavioral, morphological, and DNA sequence data have shown that the polyphagous species, *T. yuccasella*, in fact is a large species complex with species ranging in diet breadth from monophagy to feeding on as many as seven host species. Adult moths have a wingspan of 15–35 mm, and range in color from solid white to black, a mix of white and black, or sand-colored. The female has unique tentacular mouthparts at the tip of the first segment of the maxillary palp. With a single exception, all species are nocturnal. Adults, which are estimated to live 2–4 days, emerge during the flowering period of their host, and mate during their first night. Flowering host plants are likely found through a combination of visual cues and prominent floral scent cues. The female then visits yucca flowers to gather pollen by dragging her tentacles across the anthers. The highly sticky pollen is compacted and then held under the head. The female next seeks out flowers where she can oviposit. *Tegeticula* species use a cutting ovipositor to insert eggs one at a time at different positions in the pistil, whereas *Parategeticula* females create grooves in petals or pedicels where eggs are laid. After oviposition, the female removes a pollen batch from her load with her tentacles, walks to the stigma, and pollinates the flower by probing 10–20 times into the stigmatic cavity. In so doing, she assures that lack of pollination will not prevent fruit formation, which is critical because seeds, or modified seed tissue, is the sole food item of yucca moth larvae. Overexploitation by the moths is prevented by selective abscission of flowers that have received many eggs, and possibly by other mechanisms as well. Depending on the species, females may lay one or many eggs per flower, but typically only a handful of larvae from any one female will exist in a fruit, in part because of egg mortality. The larva hatches from the egg within a week in most species, and feeds on developing yucca seeds during fruit maturation. The fully fed larva exits the fruit, and diapauses inside a dense cocoon in the soil for one or more years. Pupation generally takes place a few weeks before adult emergence. In one tropical species, there may be no diapause.

DNA-based phylogenetic analyses of the moths suggest an estimated minimum age of 40 million years of the obligate moth-plant mutualism, and also reveal that the pollination behavior arose shortly after the moth lineage had colonized the yuccas from the Nolinaceae, a coexisting family of woody monocots in arid regions. A rapid diversification over the past five million years in the northern part of the range gave rise to about half of the extant species, including two species that have reverted to antagonism by having lost functional tentacles and pollination behavior. Instead, they oviposit directly into yucca fruits, and rely on coexisting pollinator species for the creation of yucca seeds.

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Pollinator

The agent of pollen transfer in plants, often bees.

► Pollination and Flower Visitation

Pollution and Terrestrial Arthropods

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Pollution, the unwanted and undesirable presence of a chemical or compound, is unfortunately common. The problem is global, affecting all continents and nations, and frequently crossing natural and political boundaries. Specific occurrences may be quite localized (such as waste-water runoff from mining operations) or cover exceptionally broad geographic areas (like acidic precipitation in northern Europe or the entire northeastern USA plus adjacent regions of Canada).

Problems with pollution are not new; air and soil contamination have been reported for thousands of years. Over 2,000 years ago, the Roman poet, Horace, complained about soot damaging the walls of temples. However, the problem has become substantially worse since the Industrial Revolution, with the large scale production and transport of many toxic materials. Most countries evolve through a period of intense industrialization, where the primary goal is to raise the standard of living for the population. During this period the environmental effects of pollutants are not considered a primary concern. As countries become more affluent, the desire for improving environmental quality increases, but nationalistic concerns, economic costs of less polluting technologies, and long standing patterns of industrial production work to impede changes that can reduce contaminants. Even in situations where pollution has been largely eliminated, a "legacy" of contamination may still exist. Thus, the problem of pollution is likely to continue for the foreseeable future.

Solving our existing problems of environmental contamination and mitigating the effects of contaminants on living organisms are difficult because of the incredible variety of sources and forms of pollution. Even an abbreviated list of pollutants would include thousands of industrial by-products, pesticide residues from chemicals that have been banned from use, a variety of toxic metals and chemicals in mining waste, many compounds produced by burning fossil fuels, the by-products of warfare, chemicals used in electrical generation/transport machinery, fuel additives, as well as a host of other materials. Each pollutant has the potential to disrupt ecosystems. Some have minimal effects, others have contaminated soils so that plants or animals from these areas cannot be eaten. A few have created wastelands, where the ground has become too toxic to support even the most basic organisms in an ecosystem.

Terrestrial arthropods are critical to the functioning of ecosystems. Because they are at the base of the food web, changes in population densities of arthropods can have profound effects on higher level organisms that depend on them. Insects and their relatives are used as food by many birds and mammals. Many arthropods are beneficial, serving to keep pest populations under control, thereby preventing damaging outbreaks. Others pollinate plants, disseminate seeds, and produce structures used by countless other organisms. Disruption of any of these activities can have disastrous effects on an ecosystem. Thus, arthropods are often the first animals examined when ecosystems become polluted.

Interestingly, direct contact with most pollutants generally does not harm terrestrial arthropods. Populations of arthropods are more commonly affected when pollutants are ingested, or if the pollutants change the quality or quantity of their food. These effects can be either positive or negative. The following sections summarize the major types of pollutants and their effects on arthropods.

Air Pollutants

Air pollution takes many forms. Some of the more common pollutants contain products resulting from fossil fuel combustion include ozone, carbon dioxide (CO_2) and carbon monoxide (CO), acidic precipitation (acidic fogs and acid rain), and many related compounds. In nearly all scientific studies, direct exposure to high concentrations of these contaminants does not physically harm arthropods. However, air pollution can alter plant chemistry, and thereby change the nutritional value of plants or their chemical defenses against arthropods. Examples are provided for ozone, acid fog, and CO_2.

Ozone is a remarkably active compound generated when combustion products from fuel are exposed to sunlight. Even moderate levels of ozone can damage plants and cause modifications in the form and content of plant nutrients. Exposure to ozone often increases availability of a key nutrient, nitrogen, which is critical for arthropod growth. This nutrient is very important, and frequently determines how fast an arthropod can grow, and if it will survive. Thus, insects such as the tomato pinworm, a key agricultural pest throughout the southern United States and Mexico, grow about 10% faster and survive at twice the rate if feeding on plants exposed to ozone. If ozone exposure is very high, then plants can become so damaged that arthropod populations can no longer survive. Like many toxic substances, the concentration of the contaminant, and the duration of exposure will determine if the pollutant is a benefit or detriment to arthropods.

The levels of CO_2 in the earth's atmosphere have been increasing dramatically since the industrial revolution. CO_2 concentration in the atmosphere has increased from 270 to 280 ppm to the current level of 355–360 ppm. This represents an increase of ~27% in a relatively short period of time. Scientists already have shown that increasing levels of atmospheric CO_2 can have substantial effects on plant suitability for arthropods. Because arthropods (like all animals) are mostly made of nitrogen, those feeding on plants have to separate the relatively small amounts of nitrogen from plant material consisting mostly of carbon. Plants grown in elevated concentrations of CO_2 have increased levels of carbon (from the carbon availability in the CO_2), and substantially reduced amounts of nitrogen. Most arthropods respond to this problem by simply eating more plant material. Some eat twice as much. Others cannot cope with the relative lack of nitrogen, and develop more slowly or even die. Changing CO_2 levels will therefore have significant effects on the plants that arthropods can eat, and how much damage is caused by their feeding.

Acid deposition in the form of "acid rain" or acidic fogs is common in North America. Although terrestrial arthropods are not typically affected by direct exposure, their food plants are often damaged. Typical damage symptoms include lesion development, weathering of leaf surface waxes, foliar leaching, premature leaf fall, changes in plant nitrogen form and content, or even plant death. All of these can impact arthropod populations. Encounters with lesions can change arthropod feeding patterns. Leaf waxes are important cues used by some arthropods to identify a particular plant as a food source, and changes in waxes can make normally acceptable plants unrecognizable. Early leaf loss shortens the time available for leaf-feeding arthropods to develop. Changes in plant nitrogen form and content and plant defensive chemistry generally have profound impacts on arthropods. Some acidic fogs contain high levels of nitrogen, and may act as a fertilizer. In some instances this provides the arthropod with a more nutritious food source, allowing populations to increase. In other cases, the plants use the additional nitrogen to produce defensive chemicals that can suppress insect populations. The death of large areas of trees caused by acid rain and acidic fogs in eastern North America and some parts of Europe have dramatic effects on abundance of many arthropod species that survive on the affected tree species.

Pollutants that Transfer from Water to Soil

Many common water pollutants are readily transferred from water to soil or directly from water to plants. Terrestrial arthropods are then exposed to these materials. Some of the more common waterborne pollutants include hexavalent chromium, MTBE (methyl tertiary butyl ether), and selenium. Each of these widespread contaminants has different effects on insects.

Hexavalent chromium is one of the most common contact sensitizers in industrialized countries and is associated with numerous materials and processes, including chrome plating baths, chrome colors and dyes, cement, tanning agents, wood preservatives, anticorrosive agents, welding fumes, lubricating oils and greases, cleaning materials, and textile production. Due to the past and present use of chromium in so many industries, it is a widespread pollutant. When ingested, this material has been shown to cause a decrease in growth and fecundity in arthropods.

MTBE is a gasoline additive used to elevate the oxygenate level in gasoline. This helps the gasoline burn more completely, reducing the production of some contaminants associated with automobile exhaust. Unfortunately, this chemical has leaked into the groundwater at over 385,000 sites nationwide due to poorly sealed underground fuel storage tanks. MTBE has now been detected in 21% of 480 wells in regions using MTBE as a gasoline additive. In addition, findings from the National Water Quality Assessment Program indicate that MTBE is the second most frequently detected volatile organic compound in ground water and urban streams. Preliminary data suggest that this material can slow development of some arthropod species.

Selenium is found in contaminated soils throughout western North America. Soil accumulation is associated with agricultural irrigation, geochemical processes, mining, and a variety of other industrial sources and frequently results in significant effects on animal and human health. Although selenium is an essential trace nutrient important to humans and most other animals, toxicity occurs at high concentrations due to replacement of sulfur with Se in amino acids resulting in incorrect folding of the protein and consequently malformed, nonfunctional proteins and enzymes. Remediation strategies include removal of soil selenium by plant accumulation, harvest, and removal. Use of plants in soil remediation programs results in the availability of selenium to plant eating arthropods. Ingestion of selenium in plants by arthropods generally results in slowed growth, reduced egg production, and higher mortality.

Pollutants that transfer from water to the soil are likely to be long term problems for arthropods. Contaminated aquifers will be used for irrigation, and plant feeding organisms will be exposed to these pollutants throughout their lives. The long term effects of such exposures, and the possible interactions between the various water-borne contaminants, is not yet known.

The Special Case of Metals

Eighty-seven of the elements on the periodic table are considered metals or metalloids (elements which act like metals). These metals are toxic at relatively low levels to terrestrial arthropods and many other organisms. Although natural mineral deposits containing metals occur around the world, and the erosion of rocks and volcanoes release metals into the atmosphere, contamination of soils by metals is most often associated with human activity. In our industrial society, metals are one of the most commonly used raw materials. Consequently, waste-water runoff from mining, metal refining, sewage sludge, and other anthropogenic sources contain high levels of metals that pollute water and soil. Additionally, gas exhaust, energy and fuel production, smelters, and foundries emit metals as airborne particulates. Sources of contamination often contain mixtures of several metals or metalloids making analysis of the effects of any one element difficult to determine in a field setting.

Airborne particulates containing metals may land on the surface of food plants of arthropods, damaging plant photosynthetic systems and resulting in altered plant chemistry and nutrition for herbivores. Contamination of soils also allows for plant uptake of many metals making these metals available to herbivores. Additionally, decaying plant materials containing metals are consumed by soil and leaf litter dwelling arthropods. Metals have been shown to accumulate in the tissues of some arthropods making them more available to predatory and parasitic arthropods, as well as higher animals that eat arthropods. This can lead to biomagnification, where pollutants accumulate in the tissues of animals as they consume the contaminated arthropods.

Toxicity of metals to terrestrial arthropods has been demonstrated in the field as well as in the laboratory. Because metals are such a large and diverse group of elements it is not surprising that the mode of action and concentrations resulting in toxicity to terrestrial arthropods are variable. Additionally, arthropods themselves differ in their ability to tolerate environments containing metals. Some arthropods are able to excrete small amounts of metals and thereby avoid toxic effects at low levels of pollution. However, at slightly higher concentrations the presence of metals may result in their incorporation into proteins and enzymes, altering their ability to function properly in the arthropod system. Some metals interfere with metabolic pathways in arthropods resulting in reduced total body protein. Additionally, metals can affect the energy source of insects, the fat body. Collectively, these effects often result in impaired growth and development and the disruption of reproduction. Therefore, not surprisingly, arthropod abundance and species diversity are usually diminished in areas where metal pollution is present.

Conclusion

All of these pollutants, whether airborne, carried by water, or present in contaminated soil, can affect population development and survival of terrestrial arthropods. Because of this, all of these contaminants can influence how communities of arthropods, and the higher animals that feed on them, will function within ecosystems. Scientists are just beginning to understand the long term effects of these pollutants on terrestrial organisms.

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Polyacetylenes (and Their Thiophene Derivatives)

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Investigations carried out in the second half of the last century have suggested that certain secondary metabolites from plants, including polyacetylenes and their thiophene derivatives, exert photodynamic action. As discoveries are made, the number of natural photodynamic sensitizers of this group is increasing.

Structure

Polyacetylenes have a conjugated double and triple bond system, or may be biosynthetically cyclized into thiophene compounds such as α-terthienyl. The chemistry and the natural distribution of polyacetylenic compounds have been comprehensively described elsewhere (see “Naturally occurring acetylenes” by Bohlmann et al., 1973).

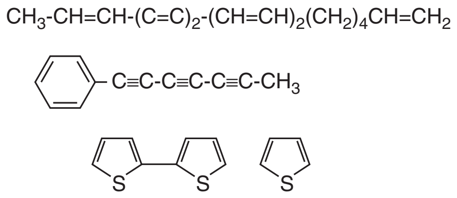
During studies on the structure activity relationship in these compounds, more than two dozen polyacetylenes and thiophene derivatives, originating from the plant family Asteraceae, have been extensively tested against various biological systems. In general, aliphatic compounds containing fewer than three conjugated acetylenic bonds do not exhibit phototoxic effects. Furthermore, in a study using the microorganisms *Escherichia coli* and *Saccharomyces cerevisiae*, it was found that thiophene derivatives generally were more phototoxic than polyacetylenes.

Occurrence in Plants

Polyacetylenes and thiophene derivatives are a very large group of secondary compounds whose photosensitizing properties in insects were first reported in 1975 by Arnason's team at the University of British Columbia in Canada. These compounds have been considered characteristic of taxonomically advanced plant families such as Asteraceae, Apiaceae, Araliaceae and Campanulaceae, as well as certain groups of Basidomycete fungi (Fig. 89). The greatest diversity is found in the Asteraceae where many polyacetylenes occur in roots, and some in the aerial parts of the members of this family.

Activity

Although the first report on the biological activity of α-terthienyl, a thiophene, as a nematocide goes back to 1958, its photoactive properties were not noticed until 1972 when the treated nematodes were exposed to near UV-A light. This was the beginning of a series of studies on the photosensitization of polyacetylenes and thiophene derivatives mediated by UV-A. Since then, numerous articles on different aspects of their activity have been published. With few exceptions, most of the studies concern insects.



Polyacetylenes (and Their Thiophene Derivatives), Figure 89 Chemical structure of polyacetylenes and their thiophenes: above, straight-chain aliphatic acetylenes (e.g., heptadeca tetraene diyne); middle, partly cyclized (e.g., PHT: phenylheptatriyne); and, below, their thiophene derivatives (e.g., α-terthienyl).

Although the photosensitizing properties of polyacetylenes on insects was reported in 1975, the presence of a polyacetylene, 8-cis-decene-4,6-diyonic acid, in insects had been recorded earlier (1968). This compound was isolated from the thoracic and abdominal glands of the cantharid beetle, *Chauliognathus lecontei*.

Twenty-four polyacetylenes (and thiophene derivatives) isolated from species in the Asteraceae were screened by Arnason and associates for their near-UV mediated larvicidal properties to *Aedes aegypti* mosquitoes. One of these, α-terthienyl that was extracted from *Tagetes,* was found to be more toxic than DDT in the presence of UV-A. Since this discovery, studies on the photodynamic action of α-terthienyl have attracted more interest.

Further studies revealed that both phenylheptatriyne (PHT) and α-terthienyl exhibited ovicidal activity against the eggs of the fruit fly, *Drosophila melanogaster*, in the dark. It was reported, however, that irradiation by UV-A respectively enhanced the toxicity by 37- and 4,333-fold.

In 1984, additional investigations on the UV-mediated activity of α-terthienyl against the tobacco hornworm, exhibited delayed and abnormal pupal formation with no subsequent adult emergence. During the same year, the first example of the inactivation of acetylcholinesterase *in vivo* by a photoactive pesticide, α-terthienyl and its two isomers, was documented by Kagan and associates. A high rate of inactivation (ca. 65–90%) occurred within a few minutes when fourth instar larvae of *Aedes aegypti* mosquitoes were treated with this phototoxin or either of its two isomers in the presence of UV-A.

In 1985, a Canadian patent was awarded covering the control of pests (algae, fungi, nematodes, or herbivorous invertebrates) by polyacetylenes. During the same year, the successful synthesis of α-terthienyl was reported. In field trials, effective control of third- and fourth-instar larvae of *Aedes* *intrudens* mosquitoes was achieved with the application of 0.1 kg/ha to natural breeding pools. This compound (α-terthienyl) was found to have a half-life of about 4 h in sunlight.

Studies on the photobiological activity of polyacetylenes and thiophene derivatives are relatively new, therefore few reports are available on their phototoxicity to organisms other than insects. Nevertheless, the broad spectrum of activity in different photoactive molecules, including dyes and furanocoumarins, is well documented. Based on a wide range of biological activity reported from several non-phototoxic studies on polyacetylenes, neither photoactive polyacetylenes nor thiophene derivatives are believed to be the exceptions. For instance, α-terthienyl (a thiophene) that has been patented for use against algae, fungi, weeds, nematodes, insects and other herbivorous invertebrates, also has been found as a potent fish poison. It also results in damage to red blood cells and human skin in the presence of UV-A. Furthermore, phenylheptatriyne (PHT), identified as the major polyacetylenic constituent of the leaves and stems of *Bidens pilosa*, is phototoxic to yeasts and bacteria when mediated by the near UV. PHT, which is present in the cuticle of *Bidens pilosa* (up to 600 ppm), strongly inhibits the germination and growth of *Fusarium culmorum* in the presence of UV, but not in the dark.

Mode of Action of Polyacetylenes and Thiophene Derivatives

In spite of over a century of research on photodynamic action, little is known about the selectivity of phototoxins. In contrast, most photoactive agents including polyacetylenes and their thiophene derivatives have shown a wide spectrum of activity. For example, many polyacetylenes and thiophene derivatives are reported to be toxic to a wide range of microorganisms and to human skin fibroblasts in the presence of UV-A. A thiophene (α-terthienyl) causes photodermatitis in human skin characterized by immediate severe erythema on exposure to sunlight and long lasting hyperpigmentation. There is evidence that this compound, in the presence of UV-A, damages DNA since it induces unscheduled DNA synthesis.

Unlike the linear furanocoumarins, e.g., 8-MOP, that kill cells by a photoinduced modification of DNA, photoactive polyacetylenes and their thiophenes attack the cell membrane by photodynamic as well as by oxygen-independent mechanisms. However, as in the case of furanocoumarins, photosensitization is mediated by the near-UV region (UV-A: 320–400 nm).

In general, straight chain aliphatic acetylenes, which are well known for their instability in vitro, have a non-oxidative mode of action that probably involves the formation of free radicals upon photoexcitation (i.e., Type I Reaction). Thiophenes, however, are Type II photodynamic photosensitizers that damage membranes via catalytic generation of singlet oxygen.

Generation of superoxide anion radicals by α-terthienyl in the anal gills of *Aedes aegypti* mosquito larvae recently has been observed. On the basis of this observation, the phototoxic action of α-terthienyl is suggested. Other investigators who have examined the metabolism of α-terthienyl in the mosquito *Culex tarsalis* found that pretreatment of the larvae with piperonyl butoxide increased larval susceptibility to α-terthienyl and reduced the rate of elimination of this substance.

Partly cyclized aromatic acetylenes such as phenylheptatriyne, which are intermediate in structure between the aliphatic compounds and the thiophenes, apparently exhibit both photodynamic and non-photodynamic processes. It was subsequently found that phenylheptatriyne and other polyacetylenes are photodynamic toward some organisms, including *E. coli*, but are partially non-photodynamic in other systems, including the microorganism *Saccharomyces*.

Most acetylenes are able to produce singlet oxygen in vitro at levels that do not fully account for their phototoxic effects. For example, after removal of oxygen, phenylheptatriyne showed only partial or no decrease in phototoxicity to microorganisms or photohemolysis of erythrocytes.

It should be mentioned that many biologically active acetylenes, such as falcarinone, falcarindiol, oenanthotoxin, capillin, *Matricaria* ester and its derivatives, and cicutotoxin, are not light-activated. Interestingly, falcarindiol, recently identified as a potent phytoalexin in fungal infections, was found to stimulate oviposition by the carrot fly, *Daucus carota*.

All photoactive representatives of dyes, furanocoumarins, polyacetylenes and their thiophene derivatives, including cercosporin and hypericin, have shown a wide spectrum of activity. For example, it has been demonstrated that furanocoumarins, upon activation by light, are powerful antimicrobial agents, nematocides, molluscicides, piscicides and powerful skin photosensitizers against man and animals.

Many polyacetylenes and thiophene derivatives recently have been shown to be toxic to a wide range of microorganisms and to human skin fibroblasts, in the presence of UV-A. A thiophene (α-terthienyl) causes serious photodermatitis in human skin, characterized by immediate severe erythema on exposure to sunlight and long lasting hyperpigmentation. There is evidence that this compound, in the presence of UV-A, damages DNA since it induces unscheduled DNA synthesis. For these reasons, there may be genetic risk associated with polyacetylenes and thiophene derivatives.

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Polyacridamide Gel Electrophoresis

A process by which molecules are separated based on their size and charge, using a polyacridamide gel and electrical current.

Polyandry

Mating of a female with several males.

Polycentropodidae

A family of caddisflies (order Trichoptera). They (as well as Psychomyiidae) commonly are known as trumpet-net and tube-making caddisflies.

► Caddisflies

Polyctenidae

A family of bugs (order Hemiptera). They sometimes are called bat bugs.

► Bugs

Polyculture

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Polyculture is the planting of two or more crops in the same field at the same time. Often the terms *polyculture* and *intercropping* are used interchangeably. However, polyculture is a broader term since it can include not only crop plants but even weeds, nursery and insectary plants, windbreaks, or hedgerows that may be intentionally included in the farming system. *Multiple cropping* is an even more inclusive term that includes both polyculture or intercropping (multiple crops grown at the same time) and crop rotation or sequential cropping (crops grown at different times). In contrast to polyculture, *monoculture* refers to a system in which only one crop is grown.

Types of Polyculture Systems

A variety of different types of intercropping systems and their combinations are possible (Fig. 90). In mixed intercropping, crops are planted without any arrangement in rows. In *row intercropping* or *strip cropping*, crops are planted in alternating rows or strips, for easier mechanization than in mixed intercropping. In *relay cropping*, one intercropped species is planted during the life cycle of another crop plant. Vining crops such as beans or cucurbits planted into an existing corn crop is a common relay crop system, since the growing vines can use the mature or dead corn stalks for support. *Agroforestry* is a type of intercropping system (either mixed or in rows) in which trees are included along with other crops. Use of hedgerows, buffer strips, and windbreaks may not be considered intercropping because they do not involve traditional crops, but they are important elements of polyculture that provide increased plant diversity in the agroecosystem.

Advantages and Disadvantages of Polyculture

Polyculture offers a number of advantages over monoculture. A crucial element for small farmers and subsistence farmers is diversification, spreading any risk of crop failure or serious damage over a number of different crops. With monoculture, the entire farm may be at risk if a serious problem affects the key crop. Intercropping systems may offer increased yield per unit of land for several reasons. Plant species with different rooting depths, light requirements, and nutrient requirements may partition and share resources more efficiently than plants of the same species. Open areas and spaces between rows are utilized more efficiently for additional crop production, which also aids in weed management. Increased plant diversity can be beneficial in managing pests, particularly herbivorous insects. On the other hand, a grower of a large monoculture has specialized in the production

Polyculture, Figure 90 **Examples of intercropping: intercropped strips of cassava and beans next to a row of sugarcane (above); windbreaks in this eggplant field provide increased border area and inject plant diversity into the system (below).**

of one crop, and may have invested heavily in equipment and infrastructure specific to that crop. Mechanization is a particular difficulty with polyculture systems, particularly mixed intercropping, which can involve substantial labor input.

Polyculture and Insect Pest Management Theory

Several hypotheses have been proposed to explain the reduction of insect pests in polyculture relative to monoculture: the disruptive-crop hypothesis, the natural enemies hypothesis, and the trap crop hypothesis. Of these, the first two appear to be more important in practice, but results vary with the specific insects and crops involved. In some systems, no advantage may be obtained by intercropping.

The *disruptive-crop hypothesis* (sometimes called the resource concentration hypothesis) states that insect herbivores are more likely to locate and remain in a concentrated patch of the host plant. Insects relying on olfactory cues from a host plant may be disrupted by strong volatiles from other plant species. Insects relying on visual cues may have difficulty in recognizing concentrations of host plants, specific vegetation colors, or backgrounds when these are disrupted by intercropped species. Once inside a patch of mixed plant species, weak fliers such as whiteflies or aphids may waste time and energy landing on or probing plants that are not optimal hosts. Highly mobile insects like some chrysomelid beetles may emigrate more quickly if preferred food plants are not easily located.

The *natural enemies hypothesis* states that potential enemies of pest insects are more abundant in mixed systems than in monoculture. This appears to be particularly true for generalist predators and parasitoids, but less so for highly specialized parasitoids that are strongly dependent on their hosts. In general, a mixed cropping system offers more sources of pollen and nectar, alternative prey, and more varied microhabitats and plant architecture to potential predators and parasitoids.

Trap cropping involves attracting a pest species away from a valuable cash crop. A classic example is the use of strips of alfalfa to attract damaging *Lygus* bugs away from cotton. More common is the use of early planting or an early maturing variety of the crop plant to attract pests, and then destroying pests and early plants before the main crop is planted. This method can preemptively remove pests and reduce insecticide costs by treating a small trap crop rather than a large field. However, use of trap crops can be risky, since improper timing or management of the trap crop can lure more pests into the area or provide a host on which pests can build up.

Polyculture for Insect Management in Practice

Farm sites can be diversified to maximize the benefits of polyculture for managing insect pests and encouraging their natural enemies. A key step is the maintenance of areas adjacent to fields as sources and refuges for beneficial insects. Natural or semi-natural areas are particularly useful for this purpose, but orchards or other perennial crops also provide permanent and stable habitat. Reduced mowing of perennial legumes and meadows can maintain important sources of pollen for hymenopterous parasitoids, and for Diptera and other predators. *Farmscaping* is a term used to describe the incorporation of hedgerows, insectary plants, cover crops, and other elements of polyculture into the overall farm design.

Edge effects from adjacent landscape are strongest at field margins. Opportunities exist to increase edge effects by subdividing large fields into smaller units, utilizing long fields or strips for crop plantings, subdividing fields with windbreaks, including strips of cover crops or insectary plants within the field, and intercropping with diverse crop species.

Many plants in the carrot (Umbelliferae), composite (Compositae), and mint (Lamiaceae) families are useful insectary plants, including important crop plants as well as many wildflowers and native plants more suitable for border or hedgerow areas. Cover crops such as buckwheat, vetch, cowpea, and various clovers are useful insectary plants as well. Aromatic herbs as intercrops may be disruptive to specialist herbivores. Plant choices for polyculture vary widely with local conditions and cropping systems, so it is necessary for growers to test and experiment locally to develop the combinations most suitable for their ecosystems.

► Flower Strips as Conservation Areas for Pest Management
► Organic Agriculture
► Conservation Biological Control
► Host Plant Selection By Insects
► Plant Extrafloral Nectaries

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Polydnaviruses (Parasitoid Related Viruses)

Members of the family Polydnaviridae are unique to insects and possess enveloped, quasicylindrical (helical symmetry) nucleocapsids which encapsidate multiple (20–30) dsDNA molecules having a composite size of 200–280 kbp. Historically, these viruses were originally placed in subgroup D of the family Baculoviridae. Polydnaviruses replicate exclusively in the nuclei of the calyx cells located in the female reproductive tract of adult hymenopterans. Two genera of polydnaviruses are recognized: the *Bracovirus and Ichnovirus* detected in braconids and ichneumonids, respectively. Bracoviruses are rod-shaped, have a width of 35–40 nm, and can vary in length from 30 to 200 nm. The nucleocapsids are enveloped by a single unit membrane (one or more nucleocapsids/membrane) that is formed de novo in the nuclei of calyx cell. Progeny bracoviruses are released through cytolysis of calyx cells. Ichnoviruses have a fusiform morphology (about 100–350 nm), possess a lenticular nucleocapsid, and contain a two-unit membrane, the first formed in the nucleus and the second acquired via budding through the cell membrane of infected calyx cells. Both the bracoviruses and ichnoviruses are complex particles and contain 20 to more than 30 structural proteins ranging from 10 to 100 kDa.

The key characteristic of the polydnaviruses is the heterodispersed double-stranded circular DNA genome. In the mid-1970s, numerous enveloped virus particles were detected in the calyx epithelial cells of the accessory glands of female parasitoids. Polydnaviruses can be purified easily from dissected calyx tissue using density gradient centrifugation methods. Polydnavirus DNA preparations applied to $CsCl_2$ gradients containing ethidium bromide produce two bands, representing the relaxed circular and superhelical DNA molecules. Kleinschmidt spreads of these preparations revealed a complex of circular DNA molecules ranging from 1.5 to 8.0 × 10^6 Da. Agarose gel electrophoresis of polydnavirus DNA preparations produced more than twenty bands ranging from 2 to more than 28 kbp. The bands detected in these gels were present in non-equimolar ratios. Hybridization studies, utilizing DNA extracted from agarose gels and labeled in vitro with ^{32}P as probes for Southerns, demonstrated that more than 80% of the electrophoretically separated bands were unique DNA molecules. The relative number of DNA molecules packaged within the polydnavirus nucleocapsid differs between the *Ichnovirus* and *Bracovirus*. It has been proposed that the different *Ichnovirus* DNA molecules are encapsidated together within a single particle. However, certain bracoviruses, characterized by possessing nucleocapsids of variable length, are believed to encapsidate a single DNA molecule. Kleinschmidt spreads of DNA released from osmotically shocked preparations of the bracovirus of *Chelonus inavitus* revealed that each nucleocapsid released a single DNA molecule, suggesting the presence of a population of virions. The helical symmetry of these viruses allows for differential packaging of DNA; the longer the helix, the larger the encapsidated dsDNA fragments.

In most cases, polydnaviruses replicate in the calyx cells of female wasps and release progeny virus particles into the calyx lumen. In the calyx cells, polydnavirus morphogenesis is observed at the pupal-adult stage of wasp development and is regulated in part by 20-hydroxyecdysone. Within a specific parasitoid population, these vertically transmitted viruses are found in 100% of egg and sperm cells, suggesting a Mendalian transmission mode. In certain ichnoviruses, including the *Campoletis sonorensis* viruses (CsV) and *Hyposoter fugitivus* (HfPV), the polydnavirus DNA is integrated into the chromosomal DNA of both the parasitoid and in selected lepidopteran cell lines. Cloned polydnavirus DNA hybridized to Southern blots detected off-size fragments in REN digests of chromosomal preparations of both parasitoid and selected insect cell lines. The stable integration of complete, unarranged polydnavirus DNA into wasp chromosomes suggests that these viruses may be transmitted as proviruses. Therefore, it has been proposed that the polydnavirus has two replicative pathways. First, it exists as a linear chromosomal provirus responsible for transmission in the wasp and, secondly, as an encapsidated circular DNA produced within the calyx cells during the pupal-adult stages. The circular DNAs, packaged into virus particles, are released during oviposition into the parasitoid's host.

Deposition of polydnaviruses during oviposition into the host plays an important role in the survival and development of the parasitoid egg. Parasitoid eggs explanted from the wasp ovary and implanted into host larvae are readily recognized as non-self, encapsulated by circulating hemocytes, and killed. However, the combination of viable polydnavirus and the egg implants results in the survival and development of the parasitoid. The observed obligatory mutualism observed between polydnaviruses and their respective wasp species is unique. The polydnaviruses delivered with the parasitoid egg during oviposition do not replicate in host lepidopteran cells; nevertheless, polydnaviruses mediate dramatic changes in host physiology. In addition to the polydnavirus, wasps deliver host-modulating substances, including venom, ovarian-secreted proteins, and/or specialized teratocyte cells that may complement the activity of polydnaviruses. The polydnaviruses delivered into the lepidopteran host are able to penetrate various cell types, undergo partial transcription, and produce m-RNA and selected viral proteins within several hours of oviposition. Host granulocytes and plasmatocytes, as well as the hemopoietic tissues (hemocyte stem cells) and prohemocytes, are the primary targets of the polydnaviruses. The presence of polydnavirus causes a marked depletion of immunoresponsive cells, disrupts the actin cytoskeleton of plasmatocytes and granulocytes, and may induce apoptosis (programmed cell death) of targeted hemocytes. The disruption of cellular actin inhibits the ability of these cells to adhere to and spread over non-self, resulting in the inhibition of the encapsulation response. The polydnavirus-mediated inhibition of the host cellular defense has been shown recently to increase the susceptibility of host larvae to other disease agents such as baculoviruses. Apoptosis of the granulocytes, characterized by cellular blebbing and fragmentation of chromosomal DNA, seen as a ladder of DNA molecules on agarose gels, results in depletion of functional granulocytes. Although the polydnaviruses are able to suppress the host cellular defense, the humoral response which involves the induction and synthesis of the anti-microbial cationic proteins remains functional in the parasitized hosts.

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Polydomous

Social insects in which single colonies occupy more than one nest.

Polyembryony

Production of more than one embryo from a single egg, a condition found in some Hymenoptera in the families Braconidae, Dryinidae, Encyrtidae, and Platygasteridae.

Polyethism

Division of labor among members of a colony of social insects. This includes caste-based polyethism, wherein different forms perform different functions, and age-based polyethism, wherein individuals perform different functions as they age.

Polygenic Resistance

Resistance of a host to a "parasite" based on many genes.

Polyhedron (pl., polyhedra)

Crystal-like inclusion bodies produced in the cells of tissues affected by certain insect viruses; ordinarily the polyhedrosis-virus particles formed in the nuclei of the host cells are rod-shaped, while those formed in the cytoplasm are polyhedral or approximately spherical.

Polyhedrosis (pl., polyhedroses)

A virus disease of certain insects characterized by the formation of polyhedral inclusions in the tissues of the infected insect; if the inclusion bodies (polyhedra) are formed in the nuclei of the infected cells, the disease is known as a "nuclear polyhedrosis." If the inclusions are formed in the cytoplasm, the disease is known as a "cytoplasmic polyhedrosis."

► Baculoviruses

Polygyny

The existence of more than one egg-producing queen in a single colony. Primary polygyny is a condition wherein the queens form a colony simultaneously; secondary polygyny occurs when supplementary queens are added after the colony is founded.

► Sociality of Insects

Polymer

A chemical compound consisting of a long chain of identical or similar units.

Polymerase Chain Reaction (PCR)

A method for amplifying DNA by means of DNA polymerases such as *Taq* DNA polymerase. PCR fundamentally involves denaturing double-stranded DNA, adding dNTPs, DNA polymerase, and primers. DNA synthesis occurs, resulting in a doubling of the number of DNA molecules defined by the primers. Additional rounds of denaturation and synthesis occur, resulting in a geometric increase in DNA molecules because each newly synthesized molecule can serve as the template for subsequent DNA amplification. Modifications of the PCR reaction have been developed for special purposes. PCR is used to clone genes, produce probes, produce ssDNA for sequencing, and carry out site-directed mutagenesis. DNA sequence differences are used to identify individuals, populations, and species.

Polymitarcyidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Polymorphism

More than distinct one body form (phenotype) within the same stage of a species. Two or more genetically different classes in the same interbreeding population. (contrast with polyphenism).

Polyphaga

One of four suborders of beetles (Coleoptera), and one of two suborders that contain numerous and important beetles (the other is suborder Adephaga). It is comprised of numerous important families, including Scarabaeidae, Elateridae, Lampyridae, Cantharidae, Dermestidae, Cleridae, Coccinellidae, Tenebrionidae, Cerambycidae, and Curculionidae.

► Beetles (Coleoptera)

Polyphagidae

A family of cockroaches (order Blattodea).

► Cockroaches

Polyphagous

Feeding broadly. In herbivores, feeding on more than one family of plants.

Polyphenism in Insects and Juvenile Hormone (JH)

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Polyphenisms are adaptations of a genotype to produce different phenotypes under different environmental conditions. Polyphenisms may be considered to be a form of polymorphism. Presumably the different phenotypes favor survival in these different environments. During the past several decades there has been a growing realization that JH is widely involved in development of polyphenism in insects.

A good model for examining the importance of JH in polyphenism is tobacco hornworm, *Manduca sexta*. A black mutant race of *M. sexta* produces larvae that are black in color at temperatures between 20 and 28°C. If the larvae of this race are heat shocked (by exposure for 6 h before apolysis, the first step in molting) at the molt between the fourth and fifth instar, a range of color variants is produced, ranging from the original black to nearly normal green. Among the larvae obtained this way, a monophenic line can be obtained by selecting black larvae in each generation. Also, a polyphenic line can be obtained by selection of normal green larvae. In each generation, larvae are subjected to heat shock and segregated by color. A control line is also maintained, given heat shock in each generation, but no color segregation is practiced. The monophenic line loses response to heat treatment after about the seventh generation, i.e., the heat treatment now produces only black larvae. In the polyphenic line, the body color remains green even at 28°C. In the control line, the body color shows continuous variation between the black color of the mutant race, and nearly fully green color, indicating polygenic control of body color. When the neck and the base of the abdomen of larvae are ligated in both the monophenic line and the polyphenic line, we infer that secretions from the head are needed for melanizing the body color. JH titers in the larvae of the two selection lines are different during the sensitive period, i.e., the time for heat shock. The titer of JH in the polyphenic line after heat shock is much higher than in the monophenic line. Obviously it is the JH titer that determines the extent of melanization. Selections in the two lines clearly indicate that genes control the extent of formation and deposition of melanin in the epidermis. Observations in the control line suggest polygenic control. From this study it may be further inferred that JH acts as a "middle man" between the genome on one hand and melanin synthesis and deposition on the other.

The hornworm manipulations demonstrate that a part of genetic variability may remain masked and unexpressed in the phenotype, but an environmental change may trigger expression of this part of the genome, and consequent polyphenism. The phenomenon may help survival under changed environmental conditions and, therefore, has been referred to as "genetic accommodation." As suggested above, JH plays the role of a mediator in development of melanization.

Polyphenism is also well studied in bruchids (Coleoptera: Bruchidae). In *Callosobruchus analis* and *C. maculatus* there is a "flightless" form (referred to as "A" phase) and "flight" form (called the "B" phase). The "flight" individuals are highly melanic in body color, and those in the "flightless" phase are much less so. In both bruchid species there are also intermediate forms with intermediate states of melanization. Crowding, high temperatures, and high humidity increase the proportion of melanic forms. Under natural conditions, larval crowding in a legume store brings about significant elevation of both temperature and humidity. Selection for 10 generations in high density cultures to favor the "B" or highly melanic phase, or to favor the "A" or lightly colored phase, results in markedly different phenotypes. When selection is then relaxed, the second post-selection generation of bruchids are all "B" in "B" favored cultures, and in the "A" cultures nearly all are "A." Hence, as in the case of *Manduca sexta*, genetic control of melanization may be inferred. Occurrence of intermediate forms between "A" and "B" phases in a continuous series in an ordinary culture in either of the two bruchid species, mentioned above, suggests polygenic control of phase determination in them.

When adults of *C. analis* that have recently eclosed are treated with an extract of cockroach corpora allata, a JH analogue, or the bruchid's own JH by implantation in the abdomen with the severed heads from well-sclerotized conspecifics, the effects of JH are evident. In all these experiments, there is a significant increase in the proportion of "A" individuals, as compared to controls (which have received either application of solvents without JH or implants of coxae of legs in place of heads). That in any of these experiments 100% of the individuals do not become "A" points to polygenic control of phase determination, and shows that some individuals do not have genetic proclivity to respond to increased titer of JH.

Bruchids and other phytophagous beetles show polyphenism elsewhere in their organization. In the phase "B" males of *Callosobruchus analis* and *C. maculates*, retournement of the aedeagus is anticlockwise, while in "A" males it is clockwise. (Retournement is rotation of the male aedeagus during development about its longitudinal axis). In Phytophaga (Phytophaga = Chrysomelidae + Bruchidae + Cerambycidae), the rotation is through 180°, so that the ventral surface of the organ becomes dorsal and vice versa ("clockwise" and "anticlockwise" refer to the direction of the rotation, as seen from the caudal end). Deficiency of JH promotes appearance of the "B" phase, which is characterized both by a high degree of melanization as well as anticlockwise retournement.

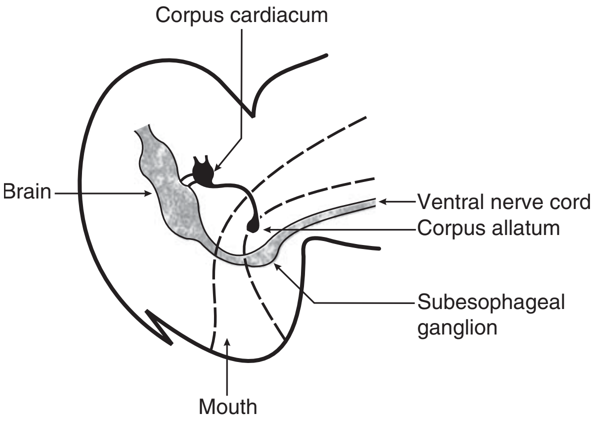
Among other insects, there are instances of polyphenism similar to what is documented in bruchids. *Zygogramma suturalis*, a chrysomelid that was introduced in northern Caucasus from North America for biological control of the ragweed *Ambrosia artemisiifolia* displays some elements of polyphenism. The introduced beetle forms a "solitary population wave" (SPW), moving ahead and effectively destroying the weed. As the SPW advances, two remarkable changes take place in the beetles: increasing melanization of the body color, and appearance of flight capacity, even though in the home country the beetle is a non-flying species. The formation of "flyers" takes place under high population density conditions within the SPW. As noted above, high population density in a bruchid culture induces appearance of "flight" and melanized individuals. If JH levels were determined in the SPW, it is likely that further resemblance with polyphenism in bruchids may be demonstrated.

JH titer is regulated by a balance between synthesis and degradation, and the degradation is brought about by the enzyme JHE (JH esterase). Higher JHE titer suppresses reproduction in the migratory phase of butterflies. The migratory phase is correlated with lowering of JH titer in several insects, including the beetles *Melolontha melolontha* and *Leptinotarsa decemlineata*. *Chrysolina aurichalcea* is a leaf beetle that normally is brachypterous and flightless. However, there are populations of this species in which some individuals fly. The flying individuals are all females with underdeveloped ovaries. Flying individuals have longer and thicker wings, and are pigmented deep red basally.

Locusts also show polyphenism similar to that of bruchids. Locusts are grasshoppers, which, under certain environmental conditions produce a swarming or migratory phase. Their swarms are formed in limited areas with vegetation, and surrounded by long stretches of arid land. When locust species multiply in such a breeding area for some time and their population density increases, darkly pigmented and more active hoppers begin to appear, replacing the green forms that predominated previously. If population densities remain high they leave the breeding area as a swarm. The involvement of corpora allata (CA), the gland that produces JH in phase determination in the locust *Locusta* (Fig. 91) , has long been known. Implantation of CA from another hopper in the body of a hopper in a crowded culture results in changes in the implant-receiving hopper, so that the adult developing from it shows characteristics of the non-swarming phase. In addition, if CA are removed in the fourth instar of *Locusta*, the dark pigmentation characteristic of the swarming phase appears in the fifth instar. Thus, in this case too, JH is involved in production of polyphenism.

The role of JH in locust phase production is limited. Juvenile hormone modulates cuticular melanization and the rate of reproductive maturation, regulating vitellogenesis at the transcriptional level and nonspecifically stimulating the translational capacity of the locust fat body. However, JH does not appear to be involved in behavioral phase transition of locusts. Long-term treatment of crowded nymphs with the JH analog methoprene does not reduce development of their gregarious behavior. So although JH induces certain solitarious characteristics such as green coloration, it is not the primary cause of phase transition.

JH influences caste differentiation in the bees. Topical application of JH on three-day-old



Polyphenism in Insects and Juvenile Hormone (JH), Figure 91 A vertical longitudinal cut through the head of *Locusta* to show location of the corpora allata.

worker honey bee larvae results in development of queen-like features. Polyploidization of CA cells through endomitosis is complete at the beginning of the fifth instar in a queen larva, and at the end of the fifth instar in a worker larva. At the end of the larval development, the CA volume in a queen larva is twice that in a worker larva. This is indicative of higher JH activity during queen bee differentiation.

Similarly, a single application of JH to the first or the second instar larva of the bumblebee, *Bombus terrestris*, in a young colony that has just been started by the queen, and in which all larvae are destined to be workers, leads to the treated larva developing into a queen. However, this treatment to older colonies does not produce a clear-cut result, as in such colonies some larvae, without any treatment, develop into queens.

The role of JH in insect polyphenism is becoming clearer. JH is involved in the control of gene switching and it exerts this control only during certain critical periods. Thus, the presence or level of JH during a critical period results in expression of alternative developmental pathways. There are relatively brief critical periods of hormone sensitivity during which the development switch occurs, although the hormone sensitive periods of different tissues occur at different times during development. It is important to note that change of environs, often with change of habitat, may alter JH concentration in the hormone sensitive period, and thus alter developmental path. Thus, it may be concluded that involvement of JH in development of polyphenism is widely found among insects. Whether it is universal among insects cannot be inferred at this stage. JH is known to be a hormone with multiple effects in the postembryonic development of insects. It seems that initiation of some programmed changes in insect's postembryonic life has become tied to certain JH concentrations, which may be regulated by sensory perception of certain environmental changes acting through the neuroendocrine integration in the region of corpora cardiaca; hence, polyphenism.

► Phase Polymorphism in Locusts
► Corazonin
► Grasshoppers and Locusts

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Polyphenism

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The condition of having two or more discrete phenotypes, without intermediates, resulting from

Polyphenism, Table 14 **Some examples of polyphenisms, the agent invoking the polyphenism, and the inductive environment that triggers the polyphenic developmental switch**

Polyphenism	Selective agent (to which the polyphenism is an adaptation)	Inducing stimulus
Seasonal	Lethal temperature, food scarcity	Photoperiod, nonlethal temperature
Phase in aphids	Food quantity or quality	Crowding, temperature, photoperiod
Phase in locusts	Food quantity or quality	Crowding, food quality
Phase in caterpillars	Predation	Food quality
Horn length	Mating success	Food quantity or quality
Wing length	Food quantity or quality	Crowding, photoperiod
Caste in ants (soldiers)	Food quantity or quality	Food quality, pheromones
Caste in ants (reproductives)	Reproduction	Pheromones, overwintering
Caste in bees	Reproduction	Nutrition, pheromones
Diapause	Lethal temperature	Photoperiod, nonlethal temperature

Adapted from Nijout, 2003

discrete phenotypic plasticity. Evolution can channel organisms into a stabilized phenotype, with little plasticity, that is well developed for a certain function or environment. Alternatively, it can lead to a more flexible phenotype, producing a robust organism. Some phenotypes show gradual change in response to environmental variation, without producing discretely different subsets, and are called "reaction norms." Some phenotypes produce discretely different (lacking intermediate forms) intraspecific variation, and this is called "polyphenism." Polyphenisms are adaptations to reliable and somewhat predictable variations in the environment. This is also known as polymorphism, especially in the older literature. Some examples are given in Table 14. Note that the inducing environment is not the same as the selective environment.

Many insects have evolved a critical period in development when they are sensitive to inducing stimuli, and this critical period occurs well in advance of the occurrence of the alternative phenotype. Thus, token stimuli such as day length signal the onset of lethal temperatures, the selective agent.

The developmental switch that leads to alternative phenotypes is regulated by hormones. Insects express both larval and adult polyphenisms. The stimulus for adult polyphenism occurs in the larval stage, and at a hormone-sensitive period an alternative development pathway is initiated. The hormones controlling polyphenic development generally are the same as those controlling molting and metamorphosis: ecdysone and juvenile hormone. The hormones trigger different patterns of gene expression, leading to alternative phenotypes.

► Castes
► Polymorphism in Locusts
► Polyphenism and Juvenile Hormone (JH)
► Phenotypic Plasticity

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Polyphyletic Group

Taxa that do not contain all the recent descendents of a single past species, but those excluded from the group are descended from a species of the group that is younger than the stem-species. Often it is difficult to distinguish paraphyletic from polyphyletic taxa.

► Phylogenetics

Polyplacidae

A family of sucking lice (order Phthiraptera). They sometimes are called spiny rat lice.

► Chewing and Sucking Lice

Polyploidy

An increase in the number of copies of the haploid genome. Most individuals are 2n, but species are known that are polyploid (3n, 4n, 5n, 6n), and such species are parthenogenetic because of the difficulty of maintaining normal meiosis. Many insect species have tissues that are polyploid, such as the salivary glands, nurse cells of the ovary, and germ line tissues.

Polypodous

Used to describe an organism with many legs. Including prolegs, caterpillar (Lepidoptera) and sawfly (Hymenoptera) larvae are polypodous. Most insects have hexapodous (six legs) larvae and a few have apodous (no legs) larvae.

Polypore Fungus Beetles

Members of the family Tetratomidae (order Coleoptera).

► Beetles

Polystoechotidae

A family of insects in the order Neuroptera. They commonly are known as giant lacewings.

► Lacewings, Antlions, and Mantidflies

Polytene Chromosomes

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Polytene chromosomes, also referred to as giant chromosomes, are huge, transversely banded ribbons of DNA. Compared with typical interphase chromosomes, they are longer by one hundred times or more and have diameters thousands of times greater. Only Collembola and Diptera among the hexapods have polytene chromosomes, which were first described in larval midges in 1881, and in Collembola in 1961. These giant chromosomes are formed in tissues that grow by cellular enlargement rather than by an increase in cell number. In contrast to a typical mitotic cycle, the homologues of polytene chromosomes typically remain paired and do not participate in the mitotic cycle of coiling and uncoiling. The sister chromatids remain paired at the end of each replication cycle, and the nuclear membrane and nucleoli remain intact throughout replication. The end product of the replication cycles is a nucleus with a haploid number of chromosomes, each containing up to 2,000 or more parallel strands. In the Collembola, however, the polytene chromosomes typically remain unpaired and the nuclei contain the diploid number (Fig. 92).

Polytene chromosomes of Diptera are found in a wide variety of larval, pupal and adult tissues, but they are best developed in tissues with a high level of secretory activity, such as the salivary glands, midgut, fat body, and Malpighian tubules. Larval salivary glands typically yield the finest preparations, as represented by the photographs of the genus *Drosophila*, which often are featured

Polytene Chromosomes, Figure 92 **Section of giant, polytene chromosome from salivary gland of larval black fly.**

in textbooks. Polytene chromosomes are also present to varying degrees in ovarian nurse cells and trichogen cells. In the Collembola, polytene chromosomes are well developed in the salivary gland cells.

The enormous size of the polytene chromosomes and the constancy of the series of light and dark bands, seen most easily in stained preparations, provide a wealth of taxonomic, phylogenetic, and genetic information. The banding patterns of the chromosomes can be photographed or drawn and then mapped by assigning sectional numbers and letters so that every band or puff can be referenced. The banding sequences tend to be species specific, with at least a segment of the total polytene complement of each species having a unique sequence of bands. These unique segments are created by one or more rearrangements, typically inversions, which reorient the sequence of bands. Nonetheless, examples of homosequential species (i.e., species with identical banding sequences) are known among taxa such as drosophilids and black flies. Inverted sequences often appear in the heterozygous condition, forming knots or loops in the chromosomes, as the sequences of each chromosomal homologue attempt to pair. An absence of heterozygous inversions in the presence of two opposite banding sequences indicates a lack of hybridization, providing evidence of reproductive isolation. Polytene chromosomes, consequently, have been used to reveal morphologically similar species (i.e., sibling species) through the absence of hybrids. The evolutionary relationships of insects also can be reconstructed on the basis of uniquely shared banding sequences. Not all Diptera have polytene chromosomes amenable to band-by-band analysis. In many taxa, the polytene chromosomes are under replicated or sticky and fragmented, making analysis of banding patterns difficult.

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Polythoridae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Polyunsaturated Fatty Acids

A dietary source of polyunsaturated fatty acids is required by many insects. Linoleic acid and linolenic acid satisfy their need. Lack of these dietary components often results in slow growth and deformed wings in the adult stage.

Pomace Flies

Members of the family Drosophilidae (order Diptera).

► Flies

Pomerantsev, Boris Ivanovich

IGOR USPENSKY
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B.I. Pomerantsev was born in St. Petersburg on March 3, 1903. Later the family moved to Saratov where he studied in a local high school. After his father died in 1917, he had to work and tried his hand at many jobs: agricultural worker, docker and sailor on the Volga River, and even a musician in a military orchestra. He left school in 1920 and entered the hydrotechnical faculty of the State University of Saratov. However, the faculty was soon closed and only in 1924 could he continue his education in the Institute of Applied Zoology and Phytopathology in Leningrad. There he began work on pyroplasmosis of cattle and ixodid ticks as vectors of the disease in Novgorod Region. He graduated from the Institute in 1929 as an entomologist specializing in ticks. From 1930 through 1933 he worked in the All-Union Institute of Plant Protection in the Department of Stock-Raising Pests, and in 1934 he was invited to the Department of Parasitology of the Zoological Institute of the USSR Academy of Sciences. Since he already had good experience in ecological studies of ticks, he concentrated his research on tick morphology and taxonomy. He collected unique material from various regions of Russia and described eight new species of ticks that remain valid today. While preparing the monograph on ixodid ticks of the USSR, he presented important arguments for his classification of ticks and considered the directions of tick evolution. He was excellent in drawing and illustrated all his scientific works. In 1939 he worked in the Far East of the USSR studying tick-borne encephalitis, a severe viral infection which emerged at that time. While making a survey over the taiga forest, he was bitten by many *Ixodes persulcatus* ticks, the main vectors of the virus, and despite immediate vaccination, the disease developed and he passed away on June 22, 1939. He had no time to complete his Ph.D. thesis. All his main works were published after his tragic death. Two of his basic papers and his monograph, the first of its kind in the world, were translated into English: "Basic directions of evolution of the Ixodoidea" (NAMRU3–13); "On the structure and organization of the Ixodoidea (Acarina, Parasitiformes)" (NAMRU3–55); and "Ixodid Ticks (Ixodidae)" (G. Anastos [Ed.], The American Institute of Biological Sciences, Washington, DC). Even now, these works are cited in publications concerning tick taxonomy and evolution. Two species of ticks were named after him: *Ixodes pomeranzevi* and *Dermacentor pomerantzevi*.

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Pompilidae

A family of wasps (order Hymenoptera). They commonly are known as spider wasps.

► Wasps, Ants, Bees and Sawflies

Popularity of Insects

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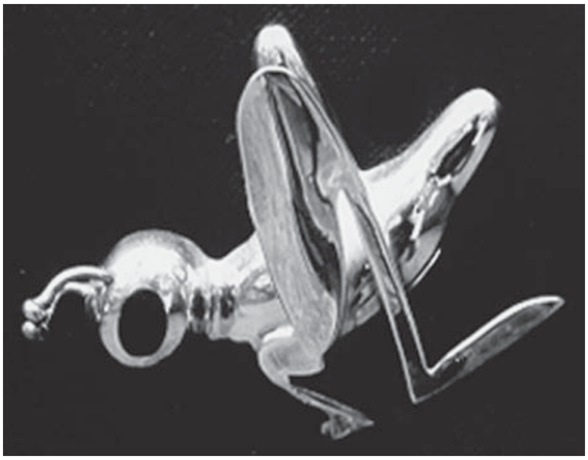
In terms of numbers of species, insects are the largest group of animals by far. There are approximately one million named species of insects, and most recent estimates suggest there are three to four million more in the world yet to be discovered. Insects also are among the most abundant in terms of sheer numbers. Dr. E.O. Wilson has estimated that there may be as many as 10,000,000,000,000,000,000 (10 quintillion) individual insects in the world.

Because of the great numbers and spectacular appearance of insects, everyone has some familiarity with them. Throughout history, insects have permeated almost every area of human society – a fact that is well documented on the web site, *Cultural Entomology Online*. Most people have some opinion, either positive or negative, about insects. Currently, insects and other arthropods are enormously popular. Everywhere one looks there is evidence of this popularity. It is virtually impossible to visit the jewelry departments of large department stores without seeing insect necklaces, pins, and earrings (Fig. 93). Also, insects are commonly featured as prints for fabrics used in women's clothes (Fig. 94). Butterflies were proclaimed to be a "fashion statement" in a recent (June 14, 2002) article in the *Life* section of *USA Today*. The article stated, "This season, butterflies are fluttering across ankle straps and purses, up-dos, and jean pockets." While butterflies are certainly the most popular insects featured in fashion, dragonflies, damselflies, bees, and ladybugs are also extremely popular.

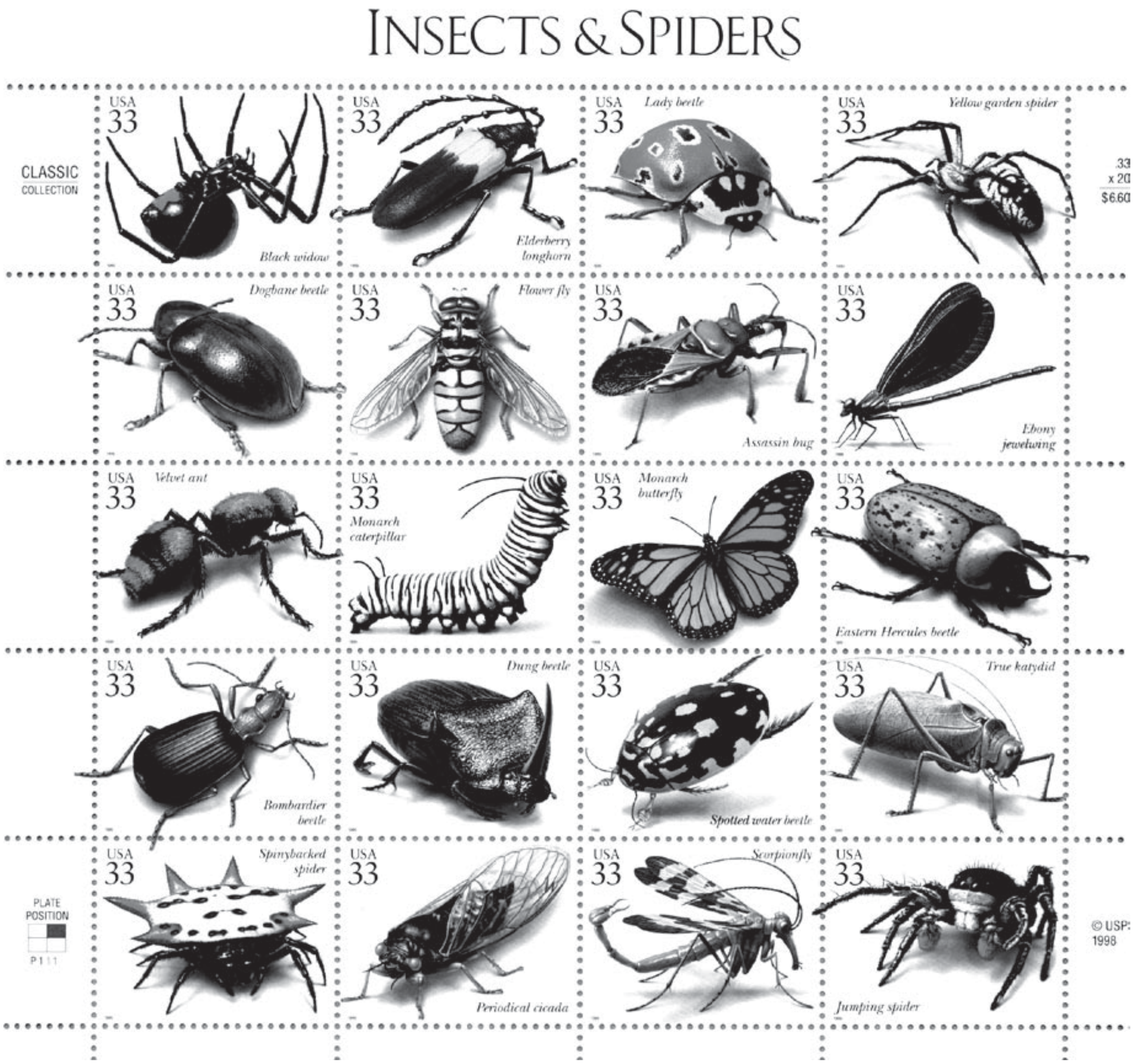


Popularity of Insects, Figure 93 **Grasshopper jewelry pin.**

Insects also are prevalent in photography and art. Kjell B. Sandved spent 24 years photographing all the letters of the alphabet and the numerals from one to nine and zero from the wings of butterflies. Many of these photographs are now featured in three magnificent posters and a book available at his butterfly alphabet web site. Even the United States Postal Service has recognized the popularity of insects. In October of 1999, the Postal Service issued a sheet of magnificent 33¢ postage stamps that featured an outstanding selection of sixteen species of insects and four species of spiders (Fig. 95). The insects and spiders sheet of stamps was ranked fourth on the Postal Service's list of the "Top 20 Commemorative Stamps of All Time."

An area of growing interest is the use of insects as human food. There are several web sites that have links to insect recipes, nutrition facts and food insect festivals. Also, there are a number of

Popularity of Insects, Figure 94 **Fabrics with butterfly and dragonfly designs.**

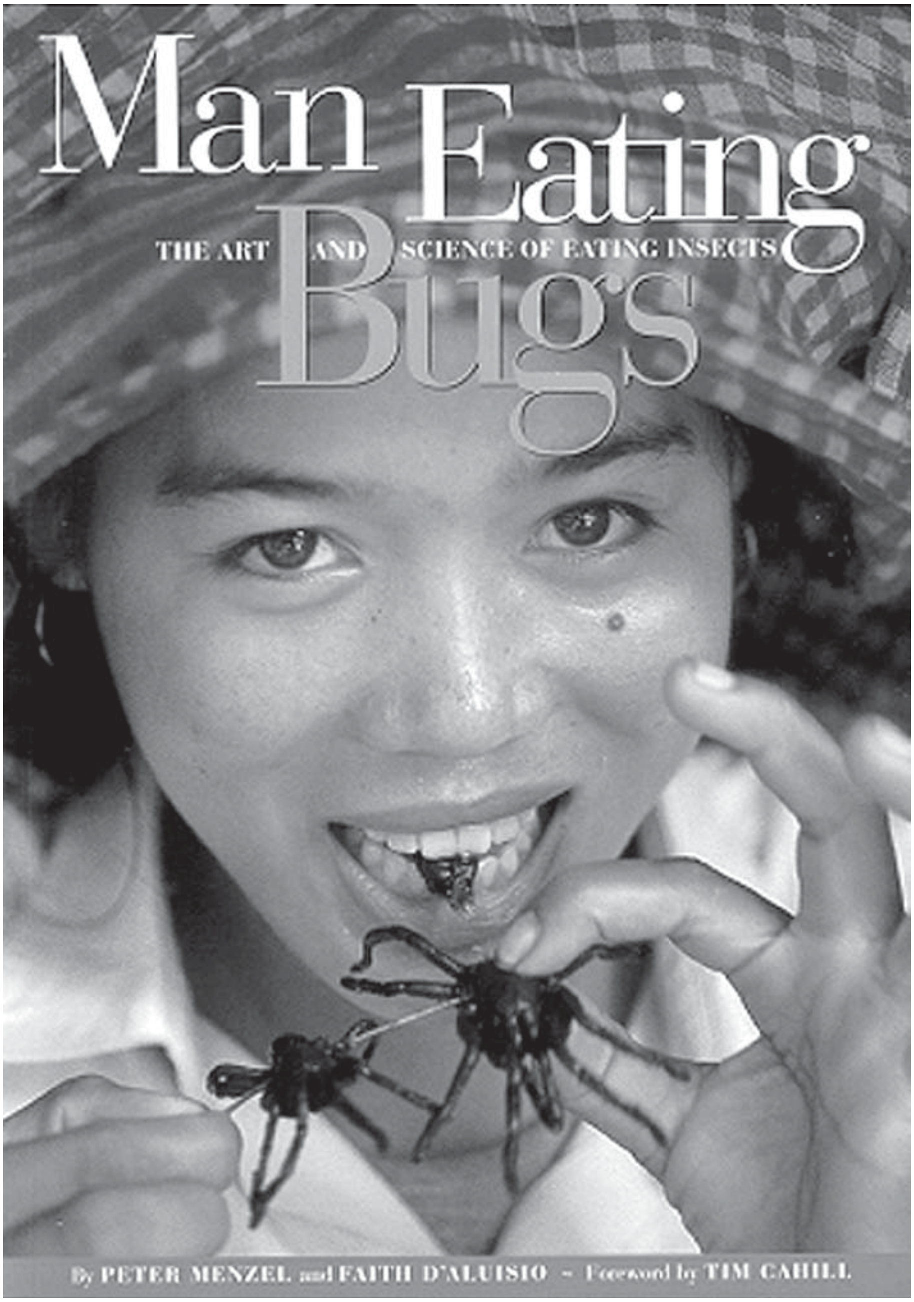


Popularity of Insects, Figure 95 **Insect and spider stamps. Stamp Design © 1999. U.S. Postal Service. Reproduced with permission. All rights reserved.**

excellent books devoted to the subject. One, *Man Eating Bugs* (Fig. 96) by Peter Menzel and Faith D'Aluisio, is a fascinating account (with numerous color pictures) of the use of insects as human food around the world.

Numerous television and magazine commercials and movies have used insects as actors. Recent popular animated movies featuring insects include PDI/Dreamworks' *ANTZ* and Pixar/Disney's *A Bug's Life*. Films with outstanding video of living insects include Galatee Films' *Microcosmos* and the BBC's outstanding three part educational video series for television, *Alien Empire*. All of these videos are currently available for purchase from online sources. Also, forensic entomology (use of insects as evidence by law enforcement agencies) has become popularized on the *Crime Scene Investigations* television series.

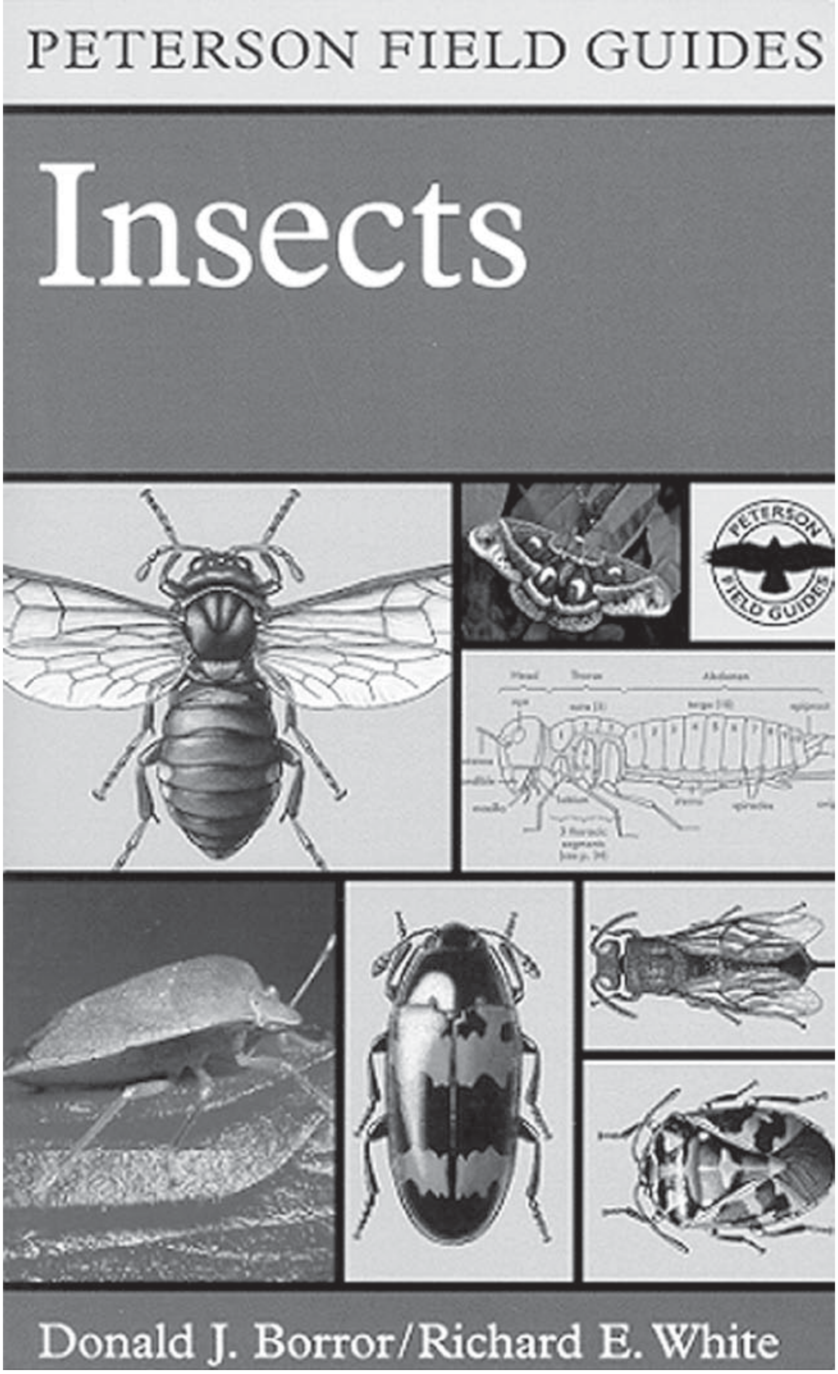
Adding to the popularity of insects is the abundance of excellent insect books for all age groups from young children to adults. For young children there are books that use insects to teach moral values and desired behaviors in addition to those that feature insect identification and behavior. For older



Popularity of Insects, Figure 96 **Front cover of *Man Eating Bugs*. Used with permission of Ten Speed Press.**

children and adults, there are a variety of outstanding field guides to the insects and specialized books that address a wide variety of specialized topics related to insects. Representative selections of insect books (Fig. 97) are found in the natural history sections of all of the major bookstores, or more complete lists may be found by using the search engines of online booksellers. Also, books as well as many other items (insect videos, posters, t-shirts, puppets, collecting supplies, etc.) of entomological interest are available from entomological supply catalogs – some of which are available online.

Many societies and organizations have contributed to the popularization of entomology. For children, most state 4-H programs have entomology projects, and the Boy Scouts of America has



PETERSON FIELD GUIDES

Insects

Donald J. Borror/Richard E. White

Popularity of Insects, Figure 97 **Front cover of Insects (Peterson Field Guide Series). Used with permission of Houghton Mifflin Company.**

an "Insect Study" merit badge. The Young Entomologists' Society is another excellent choice for children. National and state professional entomological societies have annual meetings – often with special outreach programs to schoolchildren in the localities where meetings are held. Many countries throughout the world have their own entomological societies. In the United States, the Entomological Society of America (ESA) is the leading entomological society. It has a wealth of educational material on its web site and sponsors educational programs for children and teachers at each of its annual meetings. Of special interest is the ESA's web page on frequently asked questions on entomology. The web addresses for ESA, other entomological societies in the United States, and those throughout the world are found in the accompanying Table 15 of web addresses.

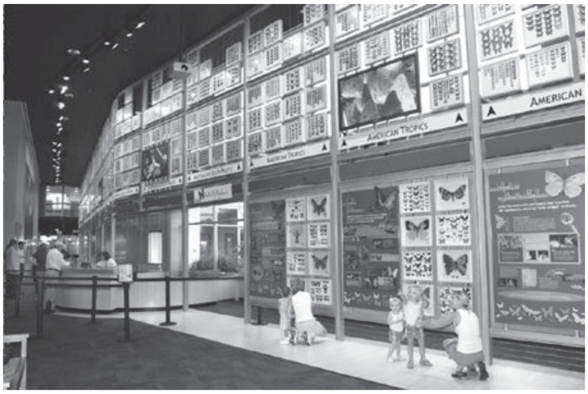
The success of insect zoos and butterfly pavilions are testimonials to the current popularity of insects. In contrast to most museums that may house millions of dead insects, the zoos and butterfly pavilions display live insects. In the case of the butterfly pavilions, the butterflies are free-flying and often land on the human visitors. Many large cities either have insect zoos or are in the process of building them. The Audubon Insectarium in New Orleans bills itself as the largest freestanding museum in the United States devoted to insects, and projects an estimated annual visitation of 400,000 and an estimated economic impact for the city of $87,000,000.

The University of Florida's McGuire Center for Lepidoptera and Biodiversity in Gainesville has a screened butterfly vivarium, "The Butterfly Rainforest" (Fig. 98), with hundreds of free-flying butterflies from around the world allowing visitors to get up-close with the butterflies. There is also a

Popularity of Insects, Table 15 Selected entomological web sites

The Entomology Index of Internet Resources	http://www.ent.iastate.edu/list/
Entomological Society of America	www.entsoc.org
Entomological Societies	www.amnh.org/learn/biodiversity_counts/know_more/w_entomsoc.htm
World's Entomological Societies	www.sciref.org/links/EntSoc/eslists.htm (case sensitive)
Young Entomologists' Society	members.aol.com/yesbugs/bugclub.html
National 4-H headquarters	http://www.national4-hheadquarters.gov/
Boy Scouts of America Insect Study Merit Badge	www.usscouts.org/usscouts/mb/mb065.html
Links to University Entomology Departments	www.entsoc.org/resources/education/colleges.htm
Frequently Asked Questions on Entomology	www.entsoc.org/resources/faq.htm
Featured Creatures	creatures.ifas.ufl.edu
Best of the Bugs website	pests.ifas.ufl.edu/bestbugs
Insect Zoos, Museums, and Butterfly Gardens in North America	http://www.entsoc.org/resources/links/zoos.htm
Public Butterfly Gardens & Zoos	Butterflywebsite.com/gardens/index.cfm
NABA Butterfly Gardening Guides	www.naba.org/pubs/bgh.html
North American Butterfly Association (NABA)	www.naba.org
Butterflies and Moths of North America	www.butterfliesandmoths.org/
Y.E.S. Minibeast Merchandise Mall	members.aol.com/YESsales/mainmenu.html
Bioquip Products	www.bioquip.com
Carolina Biological Supply Company	www.carolina.com
Butterfly Alphabet Posters & Book	www.butterflyalphabet.com
The Cultural Entomology Digest OnLine	www.insects.org/ced/index.html
The Food Insects Newsletter, Inc.	www.hollowtop.com/finl_html/finl.html
The Bay Area Bug Eating Society	www.planetscott.com/babes/

Popularity of Insects, Figure 98 **University of Florida Butterfly Rainforest.**



Popularity of Insects, Figure 99 **University of Florida Wall of Wings.**

"Wall of Wings" (Fig. 99) educational exhibit that features thousands of specimens, photographs, and videos of moths and butterflies. The McGuire Center also houses the world's second largest Lepidoptera research collection.

The popularity of butterflies has spawned a lot of interest in creating butterfly gardens in city parks, K-12 schools, and home lawns. Because different butterfly species prefer different species of flowering plants as nectar sources for the adults and host plants for the caterpillars, creating a butterfly garden requires knowledge of the appropriate plants for each geographic area. To meet this need, there are many excellent regional butterfly gardening books. One may find books specific to a region at local bookstores or by searching the web sites of online booksellers. Also, there is a wealth of information on the web including a good selection of free downloadable regional butterfly gardening guides on the web site of the North American Butterfly Association (NABA). NABA also sponsors a large number of butterfly counts throughout North America. Dates and localities for the butterfly counts are found on the NABA web site. These butterfly counts are an excellent opportunity to learn the local butterflies. A number of excellent national, regional and state butterfly books with color photographs are available to assist with identification of butterflies. On the "Butterflies of North America" web site, one may select a state and see a list of links to color photographs and biological accounts of butterflies for that state.

Releasing butterflies at weddings has become a very popular but somewhat controversial practice. According to the International Butterfly Breeders Association, there are hundreds of commercial butterfly farms in the United States that raise butterflies for schools and for release at special events. Some scientists do not approve of the releases because of the potential harmful effects of the released butterflies (that may not originate from the same area in which they are to be released) mating with local butterflies. There is concern that the progeny resulting from these matings may not be as well adapted to survive. Also, the United States Department of Agriculture is concerned that some of the butterflies may pose a threat as plant pests and has proposed regulations to restrict releases of all but a few species.

Schools and universities have played a major role in educating the public about insects. Elementary school teachers frequently utilize insects in their teaching. A number of major university entomology departments offer entomology courses designed for education majors. Also entomology courses are offered at many universities as electives or to meet general education biology requirements for non-science majors. Some of these courses have enrollments of greater than 500 students per semester.

A few university entomology departments conduct insect fairs for the general public. The best

Popularity of Insects, Figure 100 Roachhill Downs at Purdue University's Bug Bowl.

Popularity of Insects, Figure 101 Cricket-spitting at Purdue University's Bug Bowl.

of these is Purdue University's "Bug Bowl" (Fig. 100) organized by Professor Tom Turpin. Over 12,000 people attend Bug Bowl each year. These fairs offer a combination of hands-on educational experiences and entertainment. Two of the most popular events at Bug Bowl are "Roachhill Downs," a miniature race track with preserved cockroaches sitting in the stands, where live cockroaches race and an event that is now sweeping the nation, "cricket-spitting" (Fig. 101). The current world record for cricket spitting is 30 feet, 1 and ¼ in.

The popularity of insects is certain to continue to grow in the future. As with many other subjects, the world wide web will play a major role. There is already a wealth of information about this fascinating group of animals available online – just a few "clicks" away.

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Population

A group of individuals of one species that occupy the same area at the same time and generally interbreed.

Population Density

The number of organisms expressed as a unit of space (e.g., insects per plant, per square meter, or per cubic centimeter).

Population Dynamics

The changes in population sizes over time, and the factors responsible for these changes.

Population Ecology

The study in time and space of populations, their density and distribution, relative to factors causing changes in the populations.

Population Index

A sampling method that attempts to provide an indirect estimate of population density based on an associated product (e.g., frass) or effect (e.g., defoliation).

► Sampling Arthropods

Population Pyramid

A method of illustrating the age structure of a population diagrammatically by placing the youngest members of the population at the base and by stacking successive age classes above it.

Population Regulation

Maintenance of a relatively consistent population size and density. Some factor causes population density to increase when it is low, and to decrease when it is high.

Population Resilience

The ability of a population to adapt to change in its density or environment.

Pore Canal

Canals running from the epidermis through the procuticle, and used for transport of waxes, cement, and sometimes other substances to the surface (epicuticle) of the insect. The pore canals do not penetrate the epicuticle, though smaller canals called wax channels do penetrate the epicuticle.

► Cuticle

Porrect

Labial palps that protrude straight forward (not curved upward) in a pronounced manner, such as is found in Pyralidae.

Post-Emergence Treatment

Treatment of a plant, usually with a pesticide, after the plant has emerged from the soil.

Posterior

The hind region of the body, or referring to the end containing the anus.

Postoccipital Suture

A suture that marks the presence of an internal ridge, the postoccipital ridge, to which dorsal prothoracic muscles and head muscles are attached.

► Head of Hexapods

Postocular Area

An area of the head behind the eyes.

► Head of Hexapods

Postpetiole

The second segment of the "waist" (petiole) of an ant.

Post-Plant

Reference to treatments applied to a crop after planting.

Postscutellum

A small portion of the thoracic notum immediately behind the scutellum.

► Thorax of Hexapods

Potamanthidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Potamocoridae

A family of bugs (order Hemiptera).

► Bugs

Potato Aphid, *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae)

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Potato aphid is a highly variable species, and may eventually be shown to be a species complex. The origin of potato aphid is thought to be North America, though it is now found widely around the world.

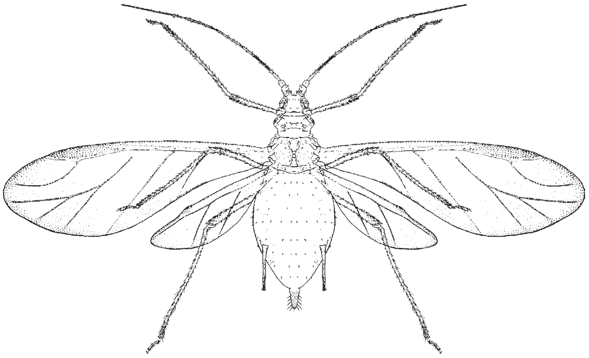
Life History

In northern areas this aphid has a sexual component to its life cycle and overwinters in the egg stage. In the spring this aphid feeds on rose, where 2–6 generations are completed. The aphids abandon the rose in the summer months and fly or walk to other suitable hosts, where several additional generations occur and high densities are attained. In the autumn, the winged forms disperse, usually back to rose. On rose, autumn migrant females, oviparous (egg-laying) females and males are found, mating occurs, and overwintering eggs are produced by oviparous females. In mild-winter regions, the sexual form is not produced or is not the only stage overwintering, as the aphid reproduces parthenogenetically (viviparously) throughout the year.

Apparently there are five nymphal instars, the mean durations of which are1.7, 1.9, 2.1, 2.4, and 1.5 days, respectively, for apterous forms. However, four instars have also been reported.

These aphids differ considerably in appearance, not only because of the different sexual forms but because they typically produce two discrete color forms, one green and the other pink. It is not surprising, therefore, that one of the common names sometimes applied to this species is the "pink and green aphid." The most common form is the adult wingless (apterous) parthenogenetic form, which predominates during the summer months. The body is green or pink in color, and free of dark markings. The cornicles are quite long, and dark at the tips. The tubercles at the base of the antennae diverge or point outward, unlike the other common potato-infesting aphids. This aphid, in its apterous form, measures about 3.0–4.0 mm long, making this the largest of the common potato-infesting aphid species. The adult winged (alate) parthenogenetic form also is abundant in the summer, especially when aphid densities are high or the nutritional quality of the host plant dissipates. This form has the same pink or green body color with cornicles that are darker distally, but bears transparent wings with dusky veins and is slightly smaller in size, about 2.1–3.4 mm long.

In the spring in warm weather areas, winged viviparous females (Fig. 102) disperse from the winter hosts in early spring to young warm-season plants such as weeds and potato. They often remain on these hosts until the plants deteriorate, often



Potato Aphid, *Macrosiphum Euphorbiae* (Thomas) (Hemiptera: Aphididae), Figure 102 Winged adult female of potato aphid, *Macrosiphum euphorbiae* (Thomas).

from overcrowding by aphids. The hot weather of summer does not favor the aphids, and their numbers greatly diminish, but begin to increase again in the autumn. They are abundant in the winter on cool-season plants such as spinach, cole crops, and weeds. Viviparous females live for about 30 days, with 10 days in the nymphal stage and the remainder as adults. Occasionally they will survive up to 50 days. They produce, on average, about 50 young aphids, but sometimes up to 80 offspring, at a rate of about 2.5 per day.

The sexual forms also differ in appearance, both due to sexual differences and in comparison with the parthenogenetic forms. In the oviparous female, wings are absent. The head and thorax are whitish, the abdomen pinkish or greenish, and the tibiae are dark. This form measures only about 2.15 mm long. The male has wings. The male also has a dark head and thorax, with a brownish green abdomen and dark appendages. The male measures less than 1.6 mm long.

Potato aphid is polyphagous, though its predominant hosts are potato, tomato, and sometimes corn in the summer, and wild or cultivated rose in the winter and spring. Sometimes spinach and lettuce are heavily infested during the autumn months. Potato aphid may be found in association with other crops such as clover, field corn, hops, peach, pawpaw, soybean, strawberry, sugarbeet, sunflower, and tobacco. It also infests such flowers as canna, geranium, gladiolus, hollyhock, iris, lily, poppy, rose, rudbeckia, and tulip. Among the weed hosts are groundcherry, *Physalis* spp.; hoary cress, *Lepidium draba*; jimsonweed, *Datura stramonium*; lambsquarters, *Chenopodium album*; matrimony vine, *Lycium* sp.; morning glory, *Ipomoea purpurea*; pepper vine, *Solanum jasminoides*; pigweed, *Amaranthus* spp.; pepperweed, *Lepidium* spp.; plantain, *Plantago* spp.; ragweed, *Ambrosia* spp.; roundleaved mallow, *Malva rotundifolia*; shepherdspurse, *Capsella bursa-pastoris*; sow thistle, *Sonchus oleraceus*; smartweed, *Polygonum* spp.; wild lettuce, *Lactuca* sp.; and winter cress, *Barbarea vulgaris*. These aphids commonly move from host to host as the quality of the plants deteriorates due to seasonal changes. They are capable, however, of feeding indefinitely on the same hosts if the plants remain nutritionally suitable. Although rose is normally reported to be the overwintering host in cold climates, there are occasional reports that either apterae (wingless forms) or eggs are found during the winter months in cold climates on such diverse plants as asparagus, raspberry, and various weeds.

Potato aphid has many natural enemies, as is commonly the case with aphids. Most of the common ladybirds (Coleoptera: Coccinellidae), some lacewings (Neuroptera: Chrysopidae), flower flies (Diptera: Syrphidae), and the predatory midge *Aphidoletes aphidomyza* (Rondani) are reported to prey on potato aphid. Ground beetles (Coleoptera: Carabidae) affect aphid populations, but not as greatly as canopy-level predators.

Among the parasitoids of potato aphid are *Aphidius*, *Diaeretiella*, *Ephedrus*, and *Praon* spp. (all Hymenoptera: Aphidiidae) and *Aphelinus* and *Dahlbominus* spp. (both Hymenoptera: Eulophidae). Only *Aphidius nigripes* Ashmead is regularly abundant.

Several closely related species of fungi affect potato aphid, and are thought to be suppressive. Frequency of fungal epizootics is positively correlated with aphid density. High levels of rainfall, though perhaps aiding in development of epizootics, are not a necessary prerequisite.

Damage

Young tissue, usually the growing tip of the plant, is first attacked by potato aphids. As the aphids multiply they spread over the entire plant, removing plant sap throughout. The leaves take on a distorted appearance, with the leaf edges turned downward. This form of injury is typical of many aphids, on a variety of plants, but is especially evident on potato infested with potato aphid. Potato plants may die back from the tip downward, and heavy infestation can kill potato plants. Leaves may be covered with honeydew and sooty mold. At times, potato aphid can be the most important pest of potato.

On tomato, pepper, and eggplant the leaf deformities are less apparent though stunting of the growing tips is evident. The blossoms are especially preferred in the latter hosts, and blossom drop or fruit deformities may occur. Potato aphid infestation resulted in higher sunscald damage to tomato fruit, presumably due to reduced shading by foliage.

In the northwestern United States, potato aphid is very abundant on corn, often covering the lower surface of leaves. Despite its great abundance, it does not cause plant deformities and is not considered to be a serious pest on this crop. In lettuce, potato aphid may be a contaminant that reduces marketability, particularly the ability to ship the crop to other nations.

Potato aphid can transmit a large number of plant viruses, though it is not considered to be an especially effective vector. Among the viruses transmitted to potato and tomato are cucumber mosaic virus and potato virus Y.

Management

Suction traps have been used to capture winged forms of potato aphid, and although useful for determining presence of the aphids they are not very predictive of crop infestation levels. Periodic placement of plants in pots in fields, or "plant traps" has also been used in monitoring, and data obtained from plant traps correlates with suction trap estimates. Population estimates are usually attained by visual examination, although yellow water pan traps are useful for estimating invasion by alate aphids.

Foliar insecticides are applied for aphid suppression. Broad-spectrum insecticides are usually used because of the other, often more serious, pests associated with solanaceous crops. Because they are not important virus vectors, however, high numbers of aphids can be tolerated. Chemical suppression is not usually recommended unless half of the leaves are infested. Soaps, detergents, and oils can be used against aphids, but care should be taken not to burn the plants.

Studies conducted in Maine, USA, demonstrated that planting practices could influence damage to potato. Delay of planting from early May, to late May or early June, resulted in up to 90% reduction in aphid infestation. Early hilling operations, wherein row ridges are heightened with soil from the row middles, similarly deprived dispersing aphids of young plant tissue, resulting in lower aphid densities.

Cultural practices can also interfere with aphid host selection behavior. Reflective mulches, particularly aluminum mulch, are sometimes recommended for disruption of aphid invasion of crops. Evaluation of aluminum mulch in potato, however, showed that the beneficial effect of the reflective mulch was slight or of short duration, and therefore impractical. The undersowing of potato with rye grass also affects aphids, resulting in reduced aphid densities in fields with grass, and no loss in crop yield.

In northern climates, aphids deposit overwintering eggs upon wild and cultivated rose, and develop on these plants in the spring. Therefore, it is desirable to destroy, or treat with an insecticide, such overwintering sites before the aphids disperse to crops. Increasingly, aphids are shipped northward from southern climates on young plants, or overwinter in northern areas in greenhouses. Care should be taken to keep from introducing aphids into fields on transplants.

There are significant differences in susceptibility to aphid infestation among tomato, lettuce, and to a lesser degree potato, varieties. The basis for resistance in lettuce is uncertain, but butterhead varieties are less susceptible to infestation.

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Potato Flea Beetle, *Epitrix cucumeris* (Harris) (Coleoptera: Chrysomelidae)

Both adults and larvae of this small insect may damage potatoes.

► Potato Pests and Their Management

Potato Leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae)

This insect is known for its ability to inflict "hopper burn" on plants.

► Potato Pests and Their Management
► Alfalfa (Lucerne) Pests and Their Management

Potato Pests and Their Management

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Potato is one of the crops that receives the heaviest use of pesticides in the world. This over reliance on insecticides has resulted in the development of pest resistance and the emergence of pests that were previously considered to be of minor economic importance.

Potato pest integrated pest management (IPM) programs should incorporate alternatives to chemical control. Pest control decisions using an IPM approach will help to reduce production costs by decreasing pesticide use. The final result of reduced pest control costs will be higher income for growers and reduced health risks for all people involved in crop management.

Managing pests successfully, using any method, depends on being able to reliably identify and monitor pest populations at each life stage. In North America, this means principally the Colorado potato beetle, the green peach aphid, and wireworms, which are considered major potato pests in most potato growing areas.

Colorado Potato Beetle

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), is probably the most important pest in all potato-growing areas in the United States and has spread to the rest of the continent, Europe and Asia. Potato yields are reduced and plants sometimes killed by the adult and larval leaf feeding. Larvae cause most of the defoliation, consuming about four times more than the adults. Leaf feeding has the highest effect on yields when it occurs within two weeks of flowering. The few tubers produced by damaged plants are stunted and possibly unmarketable. Potato plants still can tolerate some defoliation without a yield reduction: up to 25% prior to flowering, between 10 and 15% when tubers are beginning to bulk, and up to 20% for the last 3 weeks of the growing season.

This beetle was first recognized as a potato pest in 1859. The high reproductive potential and the fact that this pest has become resistant to almost all the insecticides that have been used against it, make the Colorado potato beetle such an important pest. One possible explanation for the ability to develop resistant to many insecticides is that this beetle evolved on a family of plants (Solanaceae) that contains high concentrations of toxins, and during the evolution process the beetle developed the ability to detoxify ingested toxins.

The adult is about 10 mm long, with yellow rounded and convex wing covers (elytra) marked with 10 black stripes. The eggs are orange-yellow, and found in clusters of about 30 on the underside of leaves. The larvae are 3–12.5 mm long and have slug-like, soft-skinned, brick red to orange, humped bodies with two rows of black spots on each side, six legs and a black head.

Biology

In temperate regions, adults spend the winter buried 10–25 cm deep in the soil. Adults emerge in the spring just as the first volunteer potatoes appear. Potato fields are usually rotated; therefore, beetles emerge and feed in the same field on volunteer potatoes or weed hosts and then fly to find a new host field. Recently emerged beetles either mate close to the overwintering sites or fly to new potato fields. Females are able to retain sperm from the last season's mating, and to produce viable eggs without new copulation in the spring. Beetles are able to fly several kilometers. Colonizing beetles first feed and then oviposit within a week, depending on temperature. Females lay up to 800 eggs over a 4- to 5-week period. The extended egg laying period means that larvae may be present in the field for four to five weeks. In Idaho and the northeastern states, the eggs begin to hatch at the end of May or first week of June and hatch in 4–9 days depending upon temperatures. Young larvae remain close to the egg mass but begin to move throughout the plant as that leaf is consumed. The larvae pass through four growth stages in as little as 8–10 days with average temperatures of about 30°C, while it will take longer with lower temperatures. The fourth and final growth stage consumes three times as much as the other three stages together.

The mature larvae drop from the plant and build cells in the soil where they pupate and transform into adults in 1–2 weeks. The new summer generation of adults emerges and lays eggs in that field or an adjacent field, and then migrates to overwinter. At higher elevations, the beetle may have only a single generation or a partial second generation, which feeds only briefly and then migrates to the overwintering sites without reproduction.

Management

There are several effective ways of dealing with this pest, including cultural, biological, physical and chemical practices, several of which work best in combination. Keep in mind that potato beetle control practices in one field may affect nearby fields.

Crop Rotations

Crop rotations help in delaying or reducing beetle pressure. Planting cereal grains after potatoes aids in reducing migrations because cereals are poor launch sites for the beetles. Planting new potato fields as far from last year's fields as possible (at least 400 m) will reduce the number of immigrant overwintering beetles in the new field.

Control of Volunteers and Weeds

Because overwintering adults will need to feed before walking or flying into new fields, controlling volunteer potatoes, and weeds such as nightshades, is important, as they are a preferred and early food source for these emerging adults. This tactic does not provide complete control. Therefore, it is important to scout fields to see whether additional control methods are needed.

Other methods that have proven fairly effective are the use of plastic-lined trenches, propane flamers, and vacuums. Plastic-lined trenches are arranged on the edge of a field and beetles are trapped early in the season when they walk towards the crop and at the end of the season when they move out of the field to overwintering sites.

Chemical Control and Management of Insecticide Resistance

We currently have several insecticides that are very effective. However, as mentioned before, this pest has a great ability to develop resistance to almost all different classes of insecticides. In most cases, the choice of an insecticide is based on price, effectiveness, and ease of application. It is well known that the repeated use of the same insecticide or other insecticides from the same chemical class in the same year or in successive years will accelerate the development of resistance. With a little planning and forethought insecticide programs can be developed that will allow usage of older and newly developed insecticides for a prolonged period of time.

Mixtures of insecticides are not generally recommended. Potato beetles can develop tolerance to components of the insecticide mixture and the resultant resistance may be more permanent and more difficult to manage than one developed separately to each of the active ingredients present in the mixture.

Insecticides that are not harmful to beneficial organisms should be used because natural enemies play a major role in the management of resistance. They reduce potato beetle populations regardless of the pest's resistance and act against the selection of resistant populations.

Insecticides should only be used when needed. As mentioned before, potato plants can tolerate some defoliation without a yield reduction. Once populations become damaging, insecticides can be applied either at planting or to the foliage after emergence of the plants. Systemic insecticides applied at planting are effective not only against the beetles, but also in controlling aphids. If the systemic insecticide is no longer protecting the crop when tubers are beginning to bulk (within two weeks of flowering) a foliar insecticide application may be necessary.

It is not always necessary to spray foliar insecticides over the whole field. When crops are rotated, the arriving beetles will concentrates at the edge of the new fields and defoliated plants will be restricted to field edges. Thus, treating only this area may be adequate.

Young larvae are most susceptible to insecticides. Since the older larvae are responsible for 75% of the feeding damage, early treatment will also prevent economic damage. The foliar application will be more effective when 15–30% of the beetle eggs have hatched, and will be justified with defoliation from larvae above 10–15%.

Biological Control

Not all the Colorado potato beetle eggs deposited early in the spring will become adults. Several beneficial insects that feed on eggs and young larvae will reduce the number of adults in the first spring generation. Ground beetles, predatory stinkbugs, ladybird beetles, and collops beetles are some of the predators that may reduce potato beetle populations. There also are pathogenic fungi such as *Beauveria bassiana* and *Paecilomyces farinosus* that infect and reduce potato beetle populations. However, the limited knowledge about natural enemies and the reliance on insecticides have limited their usefulness. Natural enemies can be protected by using "biorational" approaches such as microbial insecticides, mineral and vegetable oils, neem, and fermentation-based products that are toxic only to the Colorado potato beetle. Toxins from strains of the naturally occurring bacterium *Bacillus thuringiensis* (*B.t.*) are commercially available and have good potential for use in combination with natural enemies because of their specificity to potato beetle.

Green Peach Aphid

The green peach aphid, *Myzus persicae* (Salzer) (Hemiptera: Aphididae), is a European native that occurs throughout the world on a diverse host range of over 875 species of plants. It is the most common and abundant aphids in North America. It is considered one of the most difficult insect species to control due to its high reproductive potential and diverse host range. It seriously damages many crop plants directly by feeding, and also transmits more than 100 viruses to cultivated crops. Aphid numbers may occasionally be high enough to cause damage to potato crops by excessive removal of sap, but main losses occur when it transmits potato leafroll virus (PLRV). The virus causes yield reduction and reduced quality. Green peach aphid is by far the most efficient PLRV vector.

Green peach aphid may be winged or wingless. Wingless forms are yellow-green to pinkish. Winged green peach aphids are pale or bright green with a dark head and thorax. The irregular dark patches on the abdomen are characteristic but not unique. Not all winged aphids in potato fields are green peach aphids. Many species of winged aphids that have developed on other crops or weeds may be present.

Biology

The life cycle of aphids in general is very unusual and complicated. It includes several body forms, and a sexual and an asexual mode of reproduction. Asexual reproduction occurs during the growing season when females give birth to live females (they do not lay eggs, as it is usually the case with insects) for 10–25 generations. Sexual females produce eggs in the fall.

In the north, green peach aphid overwinters as eggs on the primary host, the peach tree. However, in southern regions and during mild winters aphids can also overwinter on several weeds, such as mustards, nightshade and ground cherries.

When green peach aphid overwinters on peach and nectarine trees, wingless females known as “the stem mothers” hatch from eggs that were laid near the buds in the previous fall, and produce live nymphs without mating. Eggs may hatch in response to warm periods as early as late January or early February. At high elevations egg hatching may not occur until April. The green peach aphid remains on the host tree in the spring until leaves are fully expanded. Then, winged aphids, known as “spring migrants,” are produced. These spring migrants fly to secondary hosts, which may be weeds, crop plants or ornamentals. Up to 40,000 spring migrants may be produced on one tree.

Although long-distance, wind-aided flights are possible, most winged migrants establish colonies near the winter host if summer host plants are present. They search for suitable hosts by making a series of short random flights. When an acceptable host is located the aphid feeds and deposits as many as 20 nymphs. Then the aphid takes flight and the process is repeated.

Once hosts mature, another winged form is produced, the “summer migrant.” Summer migrants usually land in greatest numbers on the edges of potato fields. Summer development of populations is strongly influenced by weather. Sudden hot or cold periods, high winds and hard rains or hail can significantly reduce populations. Summer migrants produce nymphs that can complete development in as short as 6 days and they in turn begin producing young 2 or 3 days later. Maximum reproduction occurs at temperatures between 24 and 30°C. Reproduction is sharply reduced at temperatures above 35°C and reproduction slows as temperatures are lowered from the optimum range. Temperatures under the vine canopy, where the aphids are reproducing, are less extreme than in the open. In general, weather conditions that favor high tuber yields also favor aphid reproduction. Each aphid is capable of producing 30–80 nymphs over a period of 10–20 days. They tend to deposit nymphs on a series of plants instead of putting them all on one plant. Where population peaks result in extreme crowding, winged aphids develop and move out of the field, thereby greatly reducing numbers. Declines in populations also may be associated with periods of extremely high temperatures and with a decline in potato vine condition.

The cold weather in the fall and/or the lack of suitable hosts triggers the production of winged aphids, which will be the ones returning to the primary host. These are the "fall migrants." One type of winged migrant aphid deposits nymphs on leaves of peach trees. These nymphs develop into wingless sexual females. The other type of winged migrant is the sexual male, which mates with the wingless female. Each female then deposits 5–15 eggs on or near the axillary buds. Total number of eggs per tree is extremely variable but may exceed 10,000 in mild falls when aphid activity continues into late November.

Management

A successful integrated pest management program should include methods aimed to breaking the life cycle of this aphid, such as applying insecticides to control the aphid, and eliminating or treating overwintering and secondary hosts.

Cultural Control

The number of green peach aphids present in the spring to infest crops depends upon winter survival. The common means of overwintering is on the winter host in the egg stage. Peach trees are the most common winter hosts, although apricots and other species of *Prunus* are infested on rare occasions. Fields near commercial peach orchards, or urban areas with backyard and abandoned peach trees, usually have higher populations than those in isolated areas. If spring and summer weather are favorable for aphid development a single peach tree can potentially produce enough winged aphids to initiate economic infestations on at least 500 acres of potatoes. Removing and replacing peach and apricot trees and spraying insecticides on commercial peach orchards are valid attempts to prevent aphid buildup.

Seed production areas at high elevations and commercial production areas with severe winters are usually too cold for survival of primary host plants. However, it is not unusual to observe potato fields in these areas close to towns with high aphid populations and high PLRV incidence. This is because many of the bedding plants that homeowners buy in local greenhouses are infested with green peach aphids. In Idaho for example, a 1990 survey of bedding plants that were introduced from surrounding states and were commercially available in all seed production areas of eastern Idaho, revealed that 37% of these plants were infested with green peach aphids and, therefore, home gardens represented a major source of aphid infestations in seed production areas in that state. Aphids moving directly from home gardens to potato plantings often transport viruses because home garden potato plants often have a high rate of disease infection.

Elimination of aphids on bedding plants is a very important part in the success of any integrated pest management program of green peach aphid and PLRV. Campaigns oriented to educate home gardeners about the importance of buying and planting bedding plants with no aphids are needed.

Many winged aphids from peach trees and other sources appear before crops are available for colonization. The ground cover of overwintering orchards usually includes suitable hosts that may become heavily infested. Early infestations commonly occur on a number of weeds including species of mustards, nightshade and ground cherries. Winged forms produced on these weeds later infest crop plants, including potatoes, and high numbers may appear during a short period when one or more species of weeds dry up or mature.

Where the winters are mild, aphid colonies can survive the winter outside on plants that maintain green growth. In areas where minimum temperatures are too severe for plant growth, plants near canals, springs, or adjacent to heated buildings may be infested because of the higher minimum temperatures at these locations. This kind of overwintering occurs primarily in low elevation potato-growing areas or protected places, and except in unusually mild winters or local situations, is less important than the other two aphid sources discussed.

General insecticide application guidelines based upon aphid numbers are used in some areas. When making counts, sample several areas of a field because aphid numbers are usually highest on field margins, including weeds. Nightshades are one of the preferred weeds.

When scouting, it is important to keep in mind that green peach aphid prefers to infest lower portions of potato plants. After periods of cool cloudy weather tops of plants may be infested. Colonies will also develop on upper portions of plants where crowding occurs. Aphid reproduction is favored by dense vigorous vine growth.

Early aphid migrants not controlled on time will form colonies. Therefore, detection of few aphids and application of insecticides on time will prevent the formation of these colonies. It is important to inspect the fields every 3–4 days and watch for the presence of surviving, wingless aphids.

Biological Control

Predators, parasitoids and pathogens affect aphid populations and may keep aphids below economic levels in particular situations. The sudden decline of aphid population late in the season may be associated with several factors of which the action of predators is often dominant. However, applications of insecticides and fungicides against other potato pests reduce or even eliminate populations of natural enemies, allowing aphid populations to increase rapidly. For this reason, high populations of aphids can sometime be observed after the application of an insecticide against Colorado potato beetle and potato leafhopper.

Chemical Control and Management of Insecticide Resistance

The green peach aphid is difficult to control because of the high reproduction capacity, and because it has developed resistance to at least 69 insecticides representing all major classes. However, it is critical to control aphid in production areas with PLRV susceptible cultivars such as Russet Burbank. Most of the principles of chemical control of Colorado potato beetle explained above apply also to green peach aphid.

Alternating insecticide use among the major insecticide groups reduces the development of resistance. Some systemics can give adequate aphid control and also reduce Colorado potato beetle, wireworm, or nematode numbers. Cost of the insecticide may be an important consideration.

The effectiveness of any insecticide used intensely in an area will be reduced significantly after a few years. Preventing or reducing speed with which resistance develops depends mainly on reducing insecticide use to the bare minimum necessary for economic crop production. It is important to note that not all insecticides that kill aphids prevent virus transmission.

Timing the application of an insecticide is as critical as selecting it. Applying systemic insecticides to the soil at the time of planting effectively controls aphids. At high elevations where mid- to late-season pressure from winged aphids is light, these applications may provide season-long protection. At lower elevations, one or more foliar applications of insecticide may be necessary after about midseason. Application of foliar insecticides should begin when one to three wingless aphids per 100 leaves are detected. This is a very low threshold for most scouting programs to detect with confidence.

Wireworms

Wireworms are becoming increasingly important in several potato-growing areas in North America.

Two of the possible reasons for this are the increased rotation with grasses for the cattle industry, and the removal of insecticides with long residual activity in the soil. The adults, known as click beetles, produce little or no damage and the larval stage causes the damage to seedlings and underground parts of annual crops by feeding on seeds and tunneling potato seeds and tubers. There are 885 species of wireworms (family Elateridae) in the United States. Three species of wireworms commonly damage potatoes in western North America. The sugarbeet wireworm, *Limonius californicus* (Mannerheim), and the Pacific Coast wireworm, *L. canus* LeConte, are found in soils that have been under irrigation for three or more years. The Great Basin wireworm, *Ctenicera pruinina* (Horn), infests soils previously farmed without irrigation, in pasture, or soils recently brought under cultivation. Although crop losses from wireworms are only sporadic, these are substantial (5–25%) in some places.

Wireworm larvae are about 2.5 cm long when fully mature, hard-bodied, slender, cylindrical, glossy, small-legged, and yellow-to-light brown. They feed on potato seed pieces and underground stems during the spring. This early feeding opens the seed pieces and stems to rotting organisms, which can result in poor or weak stands of potatoes. Wireworms also burrow into developing tubers. The holes look as if they were made by stabbing the tuber with a nail and usually are lined with potato skin.

Biology

The life cycle of our most common wireworms requires 3–4 years under favorable conditions. Wireworms spend the winter in the soil either as partially grown larvae or as new adults in overwintering cells. Adults work their way to the soil surface in the spring when soil temperatures reach 13°C or above. These adults require little or no food and cause no economic damage. The female mates soon after emerging from the soil, then burrows back into the soil and lays eggs at depths of 2–20 cm in several locations. The sugarbeet wireworm prefers vegetated areas for oviposition. Infestations are often spotty because oviposition is not uniform and some localities are more favorable for larval development than others.

Wireworm larvae cause the most severe feeding damage during their second and third years. In the spring, when soil temperatures reach 13°C or above, the larvae move toward the soil surface from depths of 6–24 in. where they have spent the winter. When soil surface temperatures reach 27°C or higher, they move downward again. In irrigated fields with complete foliage cover, this higher temperature level may not be reached. During the third or fourth season, mature larvae transform to fragile pupae in earthen cells. In 3–4 weeks the pupae change to adults, which remain in the earthen cells until the following spring. Wireworms in all stages may be present in the soil during any growing season.

Management

Because of the similarities in the biology of wireworms, the same management approaches apply to all the species. USDA standards for U.S. No. 1, U.S. Commercial, and U.S. No. 2 potatoes allow only 6% external defects. These includes soil or other foreign matter, sunburn, greening, growth cracks, air cracks, scab, rhizoctonia and mechanical damage, as well as insect damage. If allowance is made for defects other than wireworm damage, only to a small percentage of wireworm injury is allowable.

Detecting wireworm infestations and determining size of wireworm populations is not easy. Baiting gives a very poor estimate of population size but is a quick way to determine whether wireworms are present. Baits have to be buried in the ground one month before planting to determine the need for insecticide treatment. If wireworms are found in baits, soil sampling can be used to estimate the population density. An understanding of wireworm larval movement in soil is needed to design an effective sampling method. There are no reliable economic thresholds for wireworms.

Carrots, corn, wheat, and coarse-ground whole-wheat flour buried about 7 cm in the soil are good baits. Wrap a few grams of flour in a scrap of nylon mesh with the tail end of the mesh protruding from the soil. Randomly place these baits or carrots in a field. Mark the bait locations clearly. The more bait locations used, the greater the chance of discovering an infestation. After 2–3 days, dig up the bait and check for wireworms. Baits are not effective in soils that are very dry, wet, or cold, or if excessive organic residue is present. Covering bait stations with dark plastic will allow sampling earlier in the season when soil temperatures are cooler.

Most of the insecticides used to control wireworms are relatively old. Wireworms can be suppressed by broadcast or band treatments, by fumigation, or with seed treatments. Usually, controlling wireworms in one crop of a 2–4 year rotation will reduce wireworm damage in the other crops. For broadcast treatments, apply granules or emulsifiable concentrates evenly over the soil and incorporate immediately. Depth of incorporation varies depending upon the insecticide selected. Granular insecticides may be used as band treatments at planting time. These should be applied in narrow bands 7–10 cm below the seed piece in the seed piece furrow at planting time. Fumigants may be used to control high wireworm populations but a combination of broadcast and band treatments may be more economical to use, depending on the pest complex. Seed treatment insecticides used to control Colorado potato beetle and green peach aphid have also proven effective at reducing wireworm damage. Keep in mind that even the best insecticides will not kill all the wireworms and a small percent of a large population could still cause economic damage.

Certain cultural control practices can also be effective. One practice is to avoid rotations that include clovers and grasses. Because soil dryness can kill many wireworms in an infested field, fallowing a field will reduce wireworm numbers, but the control achieved must be weighed against the income lost from missing a crop year. It is important to keep in mind that when soils dry out in potato fields, wireworms may seek moisture from tubers, therefore increasing the wireworm damage. Plowing a dry field during the first 10 days of August can break up the pupal cases. In fields where populations have been reduced, potatoes, a susceptible crop, should be planted the first year in rotation followed by less susceptible crops such as sugarbeets, beans or corn in the ensuing years. If wireworm populations are very high in a certain field, perhaps potatoes should not be planted in that field. Avoid planting potatoes in fields that have had several successive years of cereal grains and/or corn.

Known natural enemies of wireworms include birds, carabid and staphylinid beetles, entomopathogenic nematodes, and pathogenic fungi such as *Beauveria* sp. and *Metarhizium* sp. However, there is not much information on the real effect of these natural enemies.

Secondary Pests in Alphabetical Order

Blister Beetles

Four species of blister beetles commonly damage potato: the spotted blister beetle, *Epicauta maculata* (Say), the ash-gray blister beetle, *Epicauta fabricii* (LeConte), the Nuttall blister beetle, *Lytta nutalli* Say, and the punctured blister beetle, *Epicauta puncticollis* Mannerheim. They are elongate (1.5–3 cm) with conspicuous heads and necks. The wing covers are soft and do not completely cover the tip of the abdomen. The beetles cluster on the tips of the plants causing leaf ragging and stunted plants. Severe damage, however, is not common. The adults first appear in the summer and live about 45 days. They are usually abundant only in areas adjacent to rangeland where the larval stages are predatory on grasshopper eggs.

Check field edges in years of heavy grasshopper infestations. The beetles are strong flyers and often fly from an area before damage is detected and controls can be applied. If beetles remain in the field and continue to defoliate field edges, border sprays will eventually alleviate the problem. If defoliation remains below 10–15%, controls are probably not needed.

Cutworms and Armyworms

Cutworms are soil dwelling caterpillars having a smooth appearance, three pairs of legs and five pairs of prolegs. Some species may be up to 5 cm long when mature. The black cutworm, *Agrotis ipsilon* (Hufnagel) (gray to black upper half and distinct greasy appearance), variegated cutworm, *Peridroma saucia* (Hübner) (top line of small, pale spots more distinct on front portion), spotted cutworm, *Xestia* spp. (pairs of black oblique marks on top of last four segments) army cutworm, *Euxoa auxiliaris* (Grote) (body gray with darker top-lateral and spiracle stripes), and the red-backed cutworm, *Euxoa ochrogaster* (Guenée) (top often distinctly reddish bordered with dark bands), feed at night. During the day they can be found under clods of soil or in cracks in the ground near injured plants. The western yellowstriped armyworm, *Spodoptera praefica* (Grote), feeds during the day and like the army cutworm may migrate in mass into potato fields from adjacent crops. Cutworms either cut off stems at or below ground level or strip the foliage during the growing season. They also feed on tubers that are exposed on the surface or accessible through cracks in the soil.

Cutworms spend the winter as partly grown larvae or pupae in the soil. One to several generations occur per season depending upon which cutworm is involved. The adults are dusky-brown to gray miller moths and are commonly observed flying around lights during the warmer seasons.

Control programs are aimed only at seriously damaging infestations because natural enemies generally hold the populations in check. Some defoliation from cutworms can be tolerated. Keeping defoliation between 10 and 15% will generally prevent yield loss. Weed control in previous crops and along field edges also aids in reducing cutworm damage.

Flea Beetles

Adult western potato flea beetles, *Epitrix subcrinita* LeConte, and potato flea beetle, *Epitrix cucumeris* (Harris), seldom cause damage severe enough to warrant control but extensive leaf feeding by adults may be an indication of later tuber infestation by larvae. Injury on the surface of the potato tuber consists of rough, winding trails up to 2 mm wide and of varying length. Internal tuber injury consists of shallow, narrow brown subsurface feeding tunnels. These tunnels occur singly or in groups, and are about 1 mm in diameter and up to 6 mm deep. Fungi often fill the tunnels. When potatoes are processed, these injuries must be removed by deep peeling to prevent discolored products.

The adults are about 2 mm in length and metallic greenish-black in color. Adults are active in the spring and feed in weeds until the potato plants emerge. Small, round holes in potato leaves are indicative of adult feeding. Females scatter their eggs in the soil at the base of the potato plants. The eggs hatch in 10 days and the tiny whitish larvae feed on underground stems, roots and tubers for 3–4 weeks. There are 1 or 2 generations a year depending on location. Adult western potato flea beetles hibernate under leaves, grass or trash, on margins of fields, along ditch banks and other protected places.

The tuber flea beetle, *Epitrix tuberis* Gentner, occurs in the major potato growing areas of the Northwest except southern Idaho and eastern Oregon. Extensive leaf feeding by adults will cause defoliation of the plants and reduce tuber growth.

Adults chew small holes in leaves, and extensive feeding causes a sieve-like appearance. Severely damaged leaves turn brown and die. Flea beetles can transmit potato diseases, such as spindle tuber and brown rot, and the leaf wounds may allow entry of air or waterborne disease organisms. The appearance and life cycle of the tuber flea beetle are very similar to those of the western potato flea beetle.

Larval damage is much more severe because the larval tunnel goes up to 12 mm directly into the tuber whereas the western potato flea beetle burrows under the peel and seldom penetrates over 6 mm. Some lots of potatoes may be unsuitable for processing when damage by the tuber flea beetle is extensive.

Management

Soil applications of systemic insecticides and foliar applications of insecticides for Colorado potato beetle and green peach aphid control hold flea beetle populations to sub-economic levels.

Garden Symphylan

The garden symphylan, *Scutigerella immaculata* (Newport), is not a widespread pest, but it can limit potato production in some localities. Symphylan feeding on the root hairs and rootlets may stunt plant growth before tuber formation. Damage to developing tubers consists of tiny holes in the skin with an undercut cavity lined with hard, dark, corky tissue around each point of injury. Damaged tubers are unmarketable.

Garden symphylans are not insects but are a more primitive centipede-like animal. The adults are white and live below the surface in loose soil where they appear to constantly run in and out among the particles. Symphylans move rapidly away from light, so you must look quickly after exposing the tubers or soil to see them.

Symphylans lay their eggs in the spring or early summer in cavities in the soil. The eggs hatch in 1–3 weeks. Under favorable conditions, a new brood develops in 60 days and the adults may live for several years. Optimum temperatures for activity of symphylans are from 10 to 21°C. They readily move up and down in the soil to stay within this range.

Management

Control measures must be very thorough if root crops are to be grown in symphylan- infested soils. Fall fumigation of infested areas can be effective. Insecticides should be broadcast in the spring as close to planting as possible and thorough coverage is essential. Carefully watch the field history for symphylan damage. If damage has not occurred in other crops, damage should be minimal to potatoes.

Grasshoppers

Grasshoppers are pests of potatoes only during years when they migrate out of uncultivated areas. Usually their populations are small and their damage is inconsequential. During outbreak years they can defoliate potatoes and transmit viruses, causing spindle tuber and unmottled curly dwarf.

The several species of grasshoppers that cause the most damage to potatoes are the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), clearwinged grasshopper, *Camnula pellucida* (Scudder), and the redlegged grasshopper, *Melanoplus femurrubrum* (DeGeer).

Other species may cause local, periodic problems. Grasshoppers lay their eggs in inch-long pods, each containing 10–75 eggs, deposited slightly below the surface of the soil in late summer or fall. Each female may lay from 8 to 20 pods.

Hard uncultivated ground is preferred for ovipositing although eggs are sometimes found on the edges of cultivated fields, along ditch banks, in pastures and hay fields. The eggs hatch in the spring depending upon the weather conditions and grasshopper species. The nymphs resemble the adults, but are smaller and without wings. There is one generation per year and the nymphs become mature in summer or early fall.

Management

Control programs need to be initiated only when problems develop. In outbreak years, area-wide programs are more effective than field-by-field treatment for grasshoppers. Also, in outbreak years, watch for blister beetles that may move into the field edge and cause local defoliation.

Leafhoppers

The potato leafhopper, *Empoasca fabae* (Harris), is a North American species considered to be one of the most destructive potato pests in northeastern and midwestern United States. In the West, however, the intermountain potato leafhopper, *Empoasca filamenta* Delong, is important. Nymphs and adults of leafhoppers feed on the undersurface of potato leaves and cause a speckled or white stippled appearance on the lower leaves. Adults are wedge-shaped, green insects with white markings and are about 4 mm long. Nymphs are similar in color but are smaller and lack wings. The intermountain leafhopper does not cause "hopper burn" or leaf scorching to potatoes like the eastern potato leafhopper. The adults pass the winter in grass and weeds along the field margins and in other areas where they have at least one generation before they move to potato fields.

Management

Control measures specifically for the leafhopper in the West are rarely warranted. Soil applications of systemic insecticides for other pests effectively control the intermountain potato leafhopper. In the East, foliar applications of insecticides are warranted when potato leafhopper is abundant.

Witches' Broom and Leafhoppers

There are several diseases produced by phytoplasmas in potato. Leafhopper species in the family Cicadellidae have been implied in the transmission of phytoplasmas. Phytoplasmas are pathogens transmitted in persistent form; therefore require long periods of acquisition and an incubation period.

One of these diseases, the disease known as witches' broom, has been reported occurring sporadically in some seed production areas. This disease produces a severe halting of plant growth due to the shortening of stems, and also induces marginal chlorosis of the leaves. The plants do not produce tubers, or only some small ones with enlarged buds.

The control of the diseases caused by phytoplasmas depends exclusively on the use of seed free of these diseases. For this reason, seed must be produced in areas that are known to be free of the vector, and all plants showing some of the described symptoms must be eliminated. Tubers showing proliferation of buds must be eliminated. The control of vectors is not a practical measure and perhaps it only can be used in conditions where the vector remains in the field or forms colonies on the crop.

Leather Jackets

Severe damage by the leather jacket, *Tipula dorsimacula* (Walker), may occur in fields planted with potatoes following spring plowing of alfalfa or in low, moist, weedy areas in the field. Larvae feed on tubers, causing round punctures varying from shallow depressions to inch-deep holes.

Leather jackets overwinter in the soil as mature or nearly mature larvae. Adults emerge in the spring and deposit eggs in the vicinity of plant refuse. The larvae initially feed on the decomposing plant tissue in the soil but later transfer to developing tubers.

Mature larvae are about 3–4 cm long, gray to gray-brown, and have characteristic fleshy anal projections. Their skin resembles leather, giving rise to the common name leather jacket. The adult fly is about 2.5 cm long with long, fragile legs that may drop off when the insect is handled. Adults look like giant mosquitoes.

Management

Control consists of avoiding spring incorporation of alfalfa green manure, weed control, and water management to prevent water-soaked areas.

Loopers

The most common loopers found in potato fields are the cabbage looper, *Trichoplusia ni* (Hübner) and the alfalfa looper, *Autographa californica* (Speyer).

Damage is caused by the greenish, white-striped larvae which may be 3 cm long when mature. They differ from cutworms in that they only have three pairs of prolegs. The middle of the larva is characteristically humped up when the insect rests or moves and for this reason they are often called measuring worms. Defoliation usually starts in the middle of the plant. The adult is a gray-brown miller moth that looks like a cutworm adult. There are 2–3 generations per year.

Management

Loopers seldom become a serious pest of potatoes even though they may build up high numbers. Damage usually occurs just after the vines have gone into senescence. Loopers often are found with cutworms and are blamed for the cutworm damage because the cutworms are hidden during the day. As long as defoliation remains below 10–15%, control measures are seldom warranted. Foliar sprays applied for Colorado potato beetle will usually control loopers as well.

Lygus Bugs

Lygus bugs, *Lygus elisus* Van Duzee and *Lygus hesperus* Knight, are general feeders found on most plants and trees. Damage by lygus is the result of their sucking sap from buds and leaves. Lygus bugs inject a toxin during feeding which kills the area fed upon or causes distorted growth.

Immature lygus bugs (nymphs) are smooth glossy green insects that are similar in size to aphids, but move rapidly when disturbed. Several overlapping generations occur each year that require about 6 weeks each.

Adult lygus are 6–7 mm long, green to brown bugs with a yellow triangle on the back. They hibernate in debris in fields or field margins. The insects are strong flyers and move from field to field. They usually move into a potato field just after an adjoining field is harvested or has matured. Damage is most severe on field margins.

Management

Control is seldom necessary because lygus bugs are a sporadic pest. Damage is not often noticed until the lygus bugs have left the field.

Potato Aphid

The potato aphid, *Macrosiphum euphorbiae* (Thomas), occurs in most potato growing areas, but infestations are usually not economically important for crops grown for table stock. The aphid is an efficient vector of potato virus Y and PLRV and is therefore important to seed potato production.

The aphid overwinters in the egg stage on rose bushes. Infestations develop on this host in the spring and winged forms are produced after several generations. These fly to various summer hosts that include tomatoes, ground cherry and nightshade in addition to potatoes. Nightshade weeds are apparently the preferred host.

Infestations of potato aphids usually develop on the upper parts of potato plants. This is in contrast to the green peach aphid, which usually occurs on the lower leaves. The potato aphid is green and more elongate and larger (3–4 mm) than the green peach aphid. The cauda (tip of the abdomen) is long, extending beyond the tips of the cornicles. The cauda of the green peach aphid is less conspicuous and extends about to the tips of the cornicles. The frontal tubercles of both species are prominent but they are rounded in the potato aphid and angular, appearing boxlike, in the green peach aphid. When exposed to sunlight, potato aphids rapidly move to the opposite side of the leaf while green peach aphid will not move.

Management

Plant certified seed to avoid transmission of Potato Virus Y or plant a variety not susceptible to PVY. Other control measures are seldom warranted. The same management recommendation to reduce virus spread by green peach aphid apply also to this aphid.

Thrips

Two species of thrips are associated with foliar damage to potatoes. These species are the onion thrips, *Thrips tabaci* Lindeman, and the western flower thrips, *Frankliniella occidentalis* (Pergande). Thrips cause damage by severely scarring the undersides of leaves and "silvering" the tops of leaves. Extensive damage causes the leaves to become dry and drop. Defoliated plants never recover.

Damage by thrips is usually restricted to the outside 3–5 rows adjoining wasteland, grain or dry pastures. Occasionally small fields are totally infested. Thrips move into potato fields when alfalfa is harvested or as grass or grain hosts dry during June or July. Similar damage can be caused by windburn, blown sand or by leaves being hit directly by water from sprinklers.

Thrips are tiny, yellow, brown, or white (nymphs) insects that feed at night or on cloudy days. They rasp and puncture the leaf tissue with their saber-like mouthparts and swallow the sap together with bits of leaf tissue. During the day they are found in cracks in the soil or along leaf veins on the plants.

Management

Thrips are generally kept in check by predators and seldom become a problem. When damage occurs, the thrips population has usually declined before the cause is discovered. If thrips remain in potatoes and halt growth, control measures are warranted.

Twospotted Spider Mite

Twospotted spider mites, *Tetranychus urticae* Koch, develop some years in potato fields. Problems usually occur downwind from infested bean, corn, alfalfa or clover seed fields or along dusty roads. Spider mites damage plants by puncturing the leaf tissue with their mouthparts to extract the plant juices. Injured cells and those surrounding the injury die, causing loss of chlorophyll. The injury first looks like stippling or small blotching, turning yellowish, then brown. These injury blotches come together causing the leaf to be brittle and brown. In severe infestations brown areas can progress rapidly across the field.

Adult mites are one mm long, yellow, with a dark spot on either side of the body. Nymphs are similar but smaller. Eggs are clear, round spheres found in the feeding areas.

Spider mites overwinter as adults in the soil or in debris in fields, fencerows or field margins. The adult female emerges and lays eggs on the undersides of plant foliage in late spring. A female can lay 20 eggs a day with a total of 300 eggs during her lifetime. The eggs hatch in 3–5 days. During hot weather the young develop to adults in 7–9 days. The female spins a fine web over the leaf, which apparently protects the eggs and mites from rain and predators. In severe infestations the leaves are tied together with dirty webbing. When populations become severely crowded, mites climb to the top of a plant or post and secrete a web strand. Some mites are then carried by the wind. This is why sudden infestations commonly develop downwind from previously infested fields.

Management

Sprinkler irrigation washes the foliage, breaking webs and dislodging the mites, thereby reducing

Potato Pests and Their Management, Table 16 **Insecticides available for use against potato pests**

Class	Commercial name	Common name	Site/mode of action	Application method	Pest controlled
Biological	Raven	*Bacillus thuringiensis* var. *kurstaki*	Stomach poison	Foliar	CPB
	Novador, M-Track	*Bacillus thuringiensis* var. *tenebrionis*	Stomach poison	Foliar	CPB
	Colorado Potato Beetle Beater (Bonide)	*Bacillus thuringiensis* var. *san diego*	Stomach poison	Foliar	CPB
	Agri-Mek, Avid	Abamectin	Neurotoxin, GABA inhibitor	Foliar	CPB
	Success	Spinosad	Gamma receptor (neurotoxin)	Foliar	CPB
Botanical	Azatin XL Plus BioNeem Margosan-O Neemix	Azadirachtin	Interference with molting, repellent	Foliar	CPB
	Rotenone/Pyrethrin Spray (Bonide)	Rotenone	Respiratory enzyme inhibitors of fish and insects, not mammals	Foliar	CPB
Carbamate	Temik 15G	Aldicarb	Central nervous system/acetylcholinesterase inhibitor	At planting	Aphids, CPB
	Furadan 4F	Carbofuran	Central nervous system/acetylcholinesterase inhibitor	Foliar and at planting	Aphids, CPB, wireworms, fleabeetles
	Sevin	Carbaryl	Central nervous system/acetylcholinesterase inhibitor	Foliar	CPB, leafhoppers, fleabeetles, cutworms, armyworms
	Vydate	Oxamyl	Central nervous system/acetylcholinesterase inhibitor	In-furrow at planting or foliar	Aphids, CPB, fleabeetles
Chloronicotinyl	Admire 2F	Imidacloprid	Central nervous system/neurotoxin	In-furrow at planting or seed treatment	Aphids, CPB, leafhoppers, fleabeetles
	Genesis	Imidacloprid	Central nervous system/neurotoxin	Seed treatment	CPB
	Gaucho-MZ	Imidacloprid	Central nervous system/neurotoxin	Seed treatment	Aphids, CPB

Potato Pests and Their Management, Table 16 **Insecticides available for use against potato pests**

Class	Commercial name	Common name	Site/mode of action	Application method	Pest controlled
	Provado	Imidacloprid	Central Nervous System/ neurotoxin	Foliar	Aphids, CPB
Chloronicotinyl; pyrethroid	Leverage	Imidacloprid; cyfluthrin	Central nervous system/interferes with the nicotine type acetylcholine receptor; sodium channel	Foliar	Aphids, CPB, plant bugs, flea beetles, cutworms, loopers, leafhoppers,
Cyclodiene	Thiodan 3EC, and 50WP, Phaser 3EC and 50WSB, Endosulfan 3EC and 50WSB	Endosulfan	Central nervous system/sodium and potassium balance in neurons	Foliar and chemigation	Aphids, CPB, fleabeetles
Inorganic	Kryocide, Cryolite	Sodium aluminofluoride	Inhibits enzymes with iron, calcium or magnesium centers	Foliar	CPB
Organochlorine	Methoxychlor	Methoxychlor	Central nervous system depression	Foliar	CPB
Organophosphate	Guthion	Azinphos-methyl	Central nervous system/acetylcholinesterase inhibitor	Foliar	CPB, Leafhoppers, fleabeetles
	Diazinon	Diazinon	Central nervous system/acetylcholinesterase inhibitor	Broadcast preplant	Wireworms, fleabeetles
	Di-Syston 15%G	Disulfoton	Central nervous system/acetylcholinesterase inhibitor	In-furrow at planting	Aphids, CPB
	Di-Syston 8EC	Disulfoton	Central nervous system/acetylcholinesterase inhibitor	Foliar, may be applied by chemigation	Aphids, CPB
	Lorsban	Chlorpyrifos	Central Nervous System/cholinesterase inhibitor	At planting to postemergence	wireworms
	Monitor	Methamidophos	Central nervous system/acetylcholinesterase inhibitor	Foliar	Aphids, CPB, Fleabeetles, cutworms, armyworms
	Penncap-M	Methyl parathion	Central nervous system/acetylcholinesterase inhibitor	Foliar	CPB

Potato Pests and Their Management, Table 16 **Insecticides available for use against potato pests (Continued)**

Class	Commercial name	Common name	Site/mode of action	Application method	Pest controlled
	Thimet 15G and 20G, Phorate 20G	Phorate	Central nervous system/acetylcholinesterase inhibitor	In-furrow at planting or side dress at hilling	Aphids, CPB, wireworms, fleabeetles
	Imidan 70-WSB	Phosmet	Central nervous system/acetylcholinesterase inhibitor	Foliar	CPB, fleabeetles
Pyridine Azomethine	Fulfill	Pymetrozine	Central nervous system/interferes with the nicotinic acetylcholine receptor Anti-feeding	Foliar	Aphids
Pyrethroid	Baythroid 2	Cyfluthrin	Central nervous system/axonic poison, sodium channel disrupter	Foliar	CPB
	Ambush, Pounce	Permethrin	Central nervous system/axonic poison, sodium channel disrupter	Foliar	Aphids, CPB, leafhoppers, cutworms, armyworms
	Asana XL	Esfenvalerate	Central nervous system/axonic poison, sodium channel disrupter	Foliar	Aphids, CPB, fleabeetles, cutworms, armyworms
Second-generation neonicotinoids	Actara	Thiamethoxam	Central nervous system/interferes with the nicotinic acetylcholine receptor Anti-feeding	Foliar	Aphids, CPB, leafhoppers, wireworms
	Platinum	Thiamethoxam	Central Nervous System/interferes with the nicotinic acetylcholine receptor Anti-feeding	Soil applied	Aphids, CPB, leafhoppers, wireworms

Note: For specific rates and time of application for a given product refer to manufacturer recommendations.

populations. There are many predators that attack spider mites, but because insecticides kill many of these, mite outbreaks often follow treatments for aphids or other foliar pests. Since potatoes are usually grown under optimum conditions and spider mites prefer stressed plants, serious problems are not common.

White Grubs

The two species of white grubs that frequently damage potatoes are the carrot beetle, *Bothynus gibbosus* (DeGeer), and the ten-lined June beetle, *Polyphylla decemlineata* (Say). Both species are more abundant in sandy soils where grass sod or large quantities of organic matter, such as manure, have been plowed into the soil before potatoes are planted.

The larvae are 2.5–3 cm long, C-shaped, dirty white in color with a glossy smooth skin, brown head and six prominent legs. Their large abdomen is transparent, allowing the body contents to be seen through the skin. This stage attacks the tubers, causing feeding cavities in the potato which are from 8 to 12 mm in diameter, rough, irregularly shaped and wider than deep. In severe infestations more than half of the tuber may be consumed.

The carrot beetle has an annual life cycle while the ten-lined June beetle spends 2–3 years as a grub. Adults of both beetles are awkward flyers. During May and June they feed on leaves of trees at night, and are attracted to lights, thus the name June beetles.

Management

Control of white grubs is difficult because they are found in soils with high organic content, which tend to inactivate insecticides. Currently no insecticides are registered on potatoes for white grubs. But, wireworm materials have been somewhat effective in controlling white grubs. Good weed control may also help reduce grub damage.

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Potato Tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae)

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Potato tuberworm apparently is native to southern North America, but is now spread throughout the world in areas with warm, dry climates such as southern Europe, northern and southern Africa, India, Australia, and Central and South America. The transport of tubers infested with insects causes extensive dissemination of this pest, and also results in occurrence records where this insect does not exist permanently.

Life History

A life cycle may be completed in 15–90 days, so depending on weather the number of generations is reported to range from 2 to 13 annually. In warm climates, the generations overlap and cannot be distinguished easily. Potato tuberworm normally cannot withstand freezing, so in cold climates overwintering survival by larvae is poor except within potatoes in storage or in cull piles.

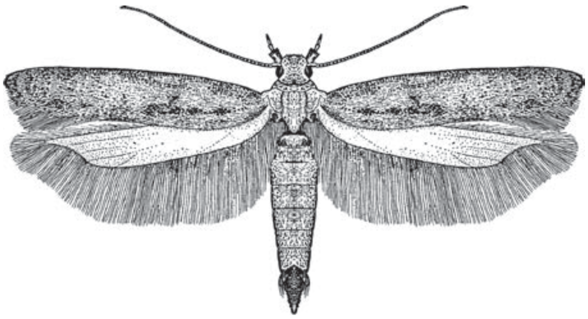
Eggs are deposited singly or in poorly defined clusters of a few eggs, usually on the underside of leaves. If deposited on potatoes in storage, however, the egg clusters tend to be larger, up to 30 eggs. Tubers tend to be heavily infested if they are exposed, i.e., not covered with soil. There also are reports of oviposition on soil adjacent to plants. The egg is elliptical in shape, and measures about 0.48 mm long and 0.36 mm wide. Initially white in color, eggs turn yellow and acquire a distinct iridescence with age. Duration of the egg stage is only about five days during the summer but may reach 30 days during cool weather.

At hatching, larvae normally begin to burrow almost immediately. Larvae normally mine the leaves, but occasionally the petioles and stems, and sometimes burrow into tubers. The older or lower leaves are preferred. Larvae often plug the entrance to their burrow with excrement, but extrude the cast skins and head capsules. Sometimes considerable amounts of silk are produced by larvae, usually when they are forced to traverse the leaf surface, but also to plug larval burrows and to web together leaves. There are four larval instars. Mean head capsule widths are about 0.20, 0.36, 0.60, and 1.13 mm for instars 1–4, respectively. Body lengths are about 1.1, 2.0, 4.5, and 7.0 mm, respectively. Mean duration (range) of the instars is about 3.5 (2–6), 2.5 (2–3), 3.1 (2–4), and 7.3 (5–12) days, respectively. Initially white in color with a black head and thoracic plate, the larva acquires additional color as it grows. In the mature larva, the head, thoracic plate and thoracic legs are black in color. The body is principally white, with pink or greenish-pink dorsally. There are five pairs of prolegs. The anal plate is yellow. Duration of the larval period may require only 14 days during the summer, but up to 70 days during the winter months.

Pupation occurs in the soil, or just beneath the epidermis of the leaf or tuber. Prior to pupation, the larva spins a silk cocoon that is usually covered with leaf trash, fecal material, soil particles, and other debris. Initially white or yellow, the pupa eventually becomes dark mahogany in color. The form of the pupa is typical of Lepidoptera, wider at the anterior end, tapering to a point at the posterior end, and with the partially developed wings twisted ventrally. The tip of the abdomen bears a hook and a circle of spines. It measures about 6 mm in length. Mean duration (range) of the pupal period is 11.6 (8–14) days.

The adult stage (Fig. 103) is a small grayish-brown moth with a wing span of 12–16 mm. The wings, especially the hind wings, are fringed. The forewings are marked with dark spots, the spots usually coalescing to form a dark longitudinal streak or a row of dark spots. The wings, abdomen, and legs also are tinged with yellow scales. The moths are nocturnal, hiding during the day beneath debris and clods of soil. Mating occurs within two days of moth emergence. Oviposition is usually completed in 6–17 days, with females each producing 150–250 eggs. Longevity rarely extends beyond 21 days. A sex pheromone has been identified and can be used for trapping under field conditions.

This insect feeds almost entirely on members of the plant family Solanaceae. Vegetable crops supporting potato tuberworm include eggplant, pepper, potato, and tomato, though potato is the only frequent host. Tobacco is sometimes affected, and potato tuberworm is sometimes called "tobacco splitworm" when it is associated with this host. Solanaceous weeds such as bittersweet, *Solanum dulcamara*; black nightshade, *S. nigrum*; groundcherry, *Physalis* spp.; henbane, *Hyoscyamus* sp.; horsenettle, *S. carolinense*; jimson weed, *Datura stramonium*; and matrimony vine, *Lycium europaeum*; also serve as hosts.

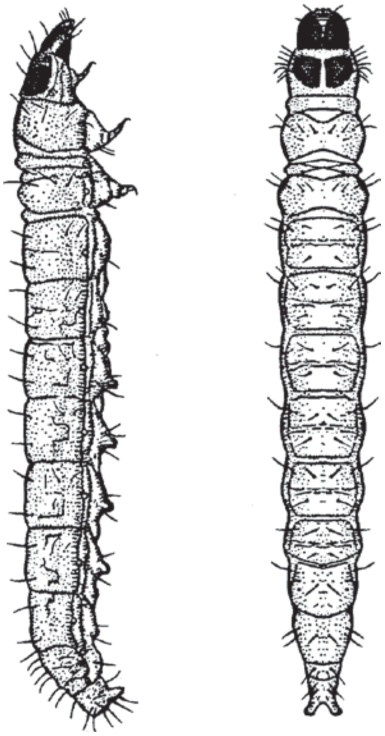


Potato Tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), Figure 103 Adult of potato tuberworm, *Phthorimaea operculella* (Zeller).

Natural enemies affect the egg, larval (Fig. 104), and pupal stages of potato tuberworm, though they are much more effective when the tuberworms are feeding on the aerial portions of the plant rather than within tubers. Among the parasitoids known to affect potato tuberworm are numerous species of Braconidae, Encyrtidae, Eulophidae, Ichneumonidae, Mymaridae, Pteromalidae, Scelionidae, and Trichogrammatidae (all Hymenoptera).

Other natural enemies are less important. Several general predators have been noted to feed on tuberworm, including the ants *Pheidole* and *Lasius* spp. (Hymenoptera: Formicidae), pirate bugs (Hemiptera: Anthocoridae), shield bugs (Hemiptera: Pentatomidae), and rove beetles (Coleoptera: Staphylinidae). Diseases have been noted, but seem to be of little natural significance.

Weather is thought to affect the abundance of potato tuberworm. Summers that are unusually warm and dry favor increase in tuberworm populations.



Potato Tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), Figure 104 **Larva of potato tuberworm, *Phthorimaea operculella* (Zeller), dorsal and lateral views.**

Damage

Leaf mining is the most common habit of potato tuberworm, but mining of the tuber or fruit is the most damaging. Mining normally is restricted to the foliage as long as it is green and succulent. Larvae may also mine the stems, usually working downward. If the tuber or fruit is attacked, the mining may occur near the epidermis, or larvae may burrow deeply. The tunnels in potato tubers normally fill with fungus. Tunneling not only destroys the food quality of the tubers, but also the sprouting potential of tubers that are to be used for propagation.

Management

Pheromone traps are effective for monitoring potato tuberworm populations, and usually there is a good correlation between trap catches and damage levels. Various types of traps can be used effectively with pheromone lures.

Tuberworm often is controlled by application of insecticide to foliage, though in some parts of the world resistance to insecticides is a problem. Also, insecticides interfere with predators and parasitoids of tuberworm, which can be quite effective, so it is prudent to determine that tuberworm is present in potentially damaging numbers before implementing an insecticide-based management effort. Biological insecticides, particularly the bacterium *Bacillus thuringiensis*, are recommended for protection of potato tubers in storage, but not usually in the field. Suppression in the field is possible with *B. thuringiensis*, but several applications may be required.

Cultural practices can greatly affect susceptibility of potato to potato tuberworm. Overwintering populations tend to be low, with tuberworm populations increasing through the year. Thus, areas where more than one potato crop are cultivated tend to experience greater loss by tuberworm, and greatest damage occurs late in the season. In some regions, potato production has been limited to the spring months to eliminate the nearly year-long availability of potatoes for tuberworm breeding.

Sanitation is extremely important in potato tuberworm management. Potatoes held in storage or in cull piles are potential sources of infestation. Similarly, potatoes left in the field, volunteer plants, and solanaceous weeds can support tuberworms. Harvested potatoes should not be left in the field overnight as this is when oviposition occurs.

If vines are killed before senescence and tubers harvested soon thereafter, the level of tuber infestation is low. Delayed harvest increases the exposure of tubers to ovipositing moths. Infestation of tubers is especially likely if there are cracks in the soil, allowing access by tuberworm. Soil depths of 5 cm or more protect tubers from infestation. Sandy soil can also be a problem if rainfall washes away soil, exposing tubers. Irrigation practices greatly affect soil condition, with furrow irrigation producing more cracks than overhead irrigation. Frequent irrigation helps to prevent soil cracking. Hilling of the soil, wherein soil is scraped from between the rows and deposited at the base of the plants, helps to deny access by tuberworm to tubers. Deep planting of potato seed, and culture of varieties that do not produce shallow tubers, also reduce incidence of tuberworm damage.

The sex pheromone can be used to manipulate populations. Mass trapping can be used to reduce damage in the field. Trapping, and disruption of mating by saturation of the atmosphere and confusion of the moths, works best for potatoes in storage.

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Potter, Charles

Charles Potter was born in England on January 3, 1907, and rose to become one of the most important workers in chemical insecticides. Beginning in the 1930s with his work on stored product pests at Imperial College, London, Potter made critical observations showing that pyrethrum formulations could be residual under the conditions of a darkened warehouse. To make proper studies of toxicity, laboratory bioassay techniques including precision spray applicators had to be developed. At the Rothamsted Experimental Station, Potter worked vigorously at developing improved techniques to assess potency of pest control materials, resulting in development of an apparatus to become known as the "Potter spraying tower." He served as head of the Insecticides and Fungicides Department, a group that grew and prospered under his direction. Potter's group was active in the introduction of organochlorine and organophosphate insecticides into commercial agriculture, and also was active in solving some of the resulting problems. They greatly improved our knowledge of structure-activity relationships, mode of action, the activities of systemic chemicals, biological and operational properties that affected efficacy, and insecticide resistance. Importantly, he remained convinced, and committed to, the notion that a synthetic material could be developed that had the beneficial attributes of natural pyrethrins. This led to development and introduction of pyrethroid insecticides, a revolutionary class of pest control materials. For his contributions to pesticide research, Potter received numerous awards and honors, including a Congressional Medal from the Third International Congress of Crop Protection, and a team award from UNESCO for development of more photostable pyrethroids. He also served as vice president of the Royal Entomological Society and president of the Association of Applied Biologists. He died on December 10, 1989.

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Potter Wasps

Members of the family Vespidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Poultry Lice

Members of the family Menoponidae (order Phthiraptera).

► Chewing and Sucking Lice

Pour-On

A type of pesticide treatment of animals wherein the liquid pesticide formulation is poured on the animal, usually in high volume.

Powassan Encephalitis

This tick-borne disease affects several species of animals.

► Ticks

Powderpost Beetles (Coleoptera: Bostrichidae: Lyctinae)

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The Lyctinae are commonly known as powderpost beetles because of the propensity of the larvae to reduce sapwood, particularly of hardwoods, into a powdery frass. The Lyctinae are worldwide in distribution, each region having an indigenous fauna plus established introduced species. They predominantly are tropical and temperate in distribution. The classification of powderpost beetles is as follows:

Order: Coleoptera
  Suborder: Polyphaga
    Superfamily: Bostrychoidea
      Family: Bostrichidae
        Subfamily: Lyctinae

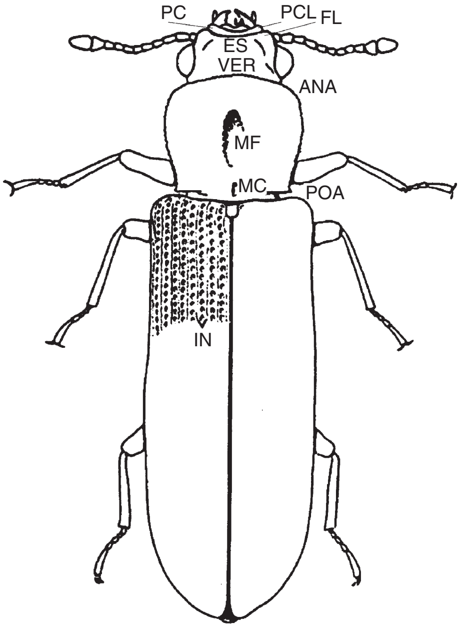
The two tribes of the Lyctinae are the lyctini and trogoxylini. the major genera of lyctini are *Lyctus, Acantholyctus*, *Lyctodon*, *Lycthoplites*, *Minthea*, *Lyctoxylon*. The major genera of trogoxylini are *Trogoxylon*, *Tristaria*, *Lyctopsis*, *Lyctoderma*, *Cephalotoma*, *Phyllyctus*. There are ~70 species of powderpost beetles, of which 11 species occur or have become established in the united states. *Lyctus planicollis* LeC., *Lyctus linearis* (Goeze), and *Trogoxylon parallelopipedum* (Melsh.) are the most common in the United States.

External Morphology

Powderpost beetles are small, 2–7.5 mm in length, reddish-brown to black beetles without distinctive spots or markings. They are elongate, body flattened dorso-ventrally, with a prominent, slightly deflexed head constricted behind the eyes. The antennae are 11-segmented, with a two-segmented terminal club, inserted immediately anterior of the eyes. The prothorax is somewhat flattened, and does not form a hood over the head (Fig. 105). The tarsi are all five-segmented, with the first segment very small and the fifth segment almost as long as all the preceding segments combined. The tarsal claws are simple.

Life History and Habits

Adult powderpost beetles are sexually mature upon emergence. Copulation occurs soon afterward. Oviposition takes place 2–3 days after mating. The female may feed on the surface of the wood by



Powderpost Beetles (Coleoptera: Bostrichidae: Lyctinae), Figure 105 **External morphology of a generalized adult powderpost beetle, dorsal aspect. ANA, anterior angle of pronotum; ES, epicranial suture; FL, frontal lobe; IN, interspace; MC, median canaliculation; MF, median fovea; PC, postclypeus; PCL, postclypeal lobe; POA, posterior angle of pronotum; VER, vertex.**

gnawing the torn fibers, possibly to detect the suitability of the timber for oviposition in relation to food value for the larvae. The female extends the long, flexible ovipositor directly into the lumen of the vessel, tracheae, or pores of the wood. The translucent white cylindrical eggs are laid in depths of from 0.5 to 1 mm. Those woods in which the vessels are most numerous are more liable to heavy attack. The diameter of the vessels in which oviposition occurs is a great importance, as it must be large enough for insertion of the ovipositor. Depending upon temperature, the incubation period may vary from 6 to 20 days. The larva, on hatching, is white and straight bodied, armed at the rear end, and with a pair of small spines. After the first molt, the larva assumes a curved form. The young larva usually tunnels with the grain of the wood. In the later stages, the larval tunnel takes an irregular course. Tunnels approaching the surface of infested wood do not penetrate it but leave a thin, unbroken layer. The larva may remain in the wood for about 10 months, the length of time varying with the temperature, moisture, and condition of the wood. The larva possesses large spiracles on the eighth abdominal segment. When fully matured, it bores its way near the surface of the wood and builds a pupal chamber. The pupal period lasts 12–30 days, though this again is variable. When transformation from pupa to adult occurs, the beetle cuts its way to the surface. When emerging, it generally pushes some of the fine dust in front of it, and as a result, small piles of dust often can be seen near new holes. These emergence or flight holes are about 2 or 3 mm in diameter.

The larva feeds mainly on the sapwood of hardwoods, such as oak, ash, hickory, mahogany and bamboo. The chief source of food of the larva is the starch in the cell content of the wood. The cell wall is not digested. Besides starch, certain sugars, disaccharides and a polysaccharide, as well as protein, are necessary constituents of the larval food. As the presence of starch in sapwood is essential for infestation to occur, the greater the starch content, the greater the possible extent of damage. Below a minimum concentration of starch, no attack occurs. Moisture also is essential for the normal development of the larva. It will thrive in wood with a moisture content of between 8 and 30%.

Predators and Parasites

Predators and parasites are not a factor in the artificial control of the powderpost beetles. Various Hymenoptera have been found to parasitize these beetles. Clerid beetles (Coleoptera) have been reported as predators.

Economic Importance

The destructiveness of powderpost beetles to wood and wood products is second only to that of termites. The annual loss of lumber and wood products runs into millions of dollars. As noted previously, powderpost larvae primarily attach to the sapwood of hardwoods. They are more often found in recently dried wood than in old wood. They attack lumber that is used for hardwood floors, crating, furniture, plywood, implement handles, and gun stocks. The damage consists of the destruction of the wood, resulting in a powdery frass as the larvae tunnel their way through the sapwood. When the adult beetles emerge, they further damage the wood by producing exit or flight holes.

Control Measures

The control of powderpost beetles in wood may be accomplished by heat treatment, fumigation, chemical treatment, and good lumber yard and saw mill sanitation.

► Wood-Attacking Insects

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Powderpost Termites

A group of termites in the family Kalotermitidae known to attack dry wood not in contact with soil, and reduce it to powder.

► Termites

Powdery Mildew

Though also wind-transmitted, these fungi also are transmitted by insects.

► Transmission of Plant Diseases by Insects

Praying Mantids (Mantodea)

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There is some debate about the most appropriate taxonomic position of praying mantids (or mantises). They are considered orthopteroid insects because they appear to have much in common with cockroaches, grasshoppers, crickets, and stick insects, all of which used to be lumped together with mantids within the order Orthoptera. Morphological and molecular evidence suggests that mantids are, in fact, most closely related to Blattodea (cockroaches) and Isoptera (termites), but most authors feel that the 1,900 or so species of mantids are sufficiently different from these groups to be classified separately: Order Dictyoptera, Suborder Mantodea. There are eight families and 28 subfamilies in this suborder:

Amorphoscelididae, containing two subfamilies from Africa and Australia

Chaeteessidae, with only one Neotropical genus, *Chaeteessa*

Empusidae, consisting of eight genera in Africa and Asia

Eremiaphilidae, ground-dwelling mantids of Africa and Asia

Hymenopodidae, with three subfamilies, including tropical flower mimics

Mantidae, the most important family with 21 subfamilies and 263 genera

Mantoididae, with a single Neotropical genus, *Mantoida*

Metallyticidae, with a single Malaysian genus, *Metallyticus*

Distinguishing Characteristics

The praying mantis (from the Greek for "prophet") derives both its name and its livelihood from the contradictory morphology and function of the prothoracic legs. When folded against the body, these appendages give the insect the appearance of prayer. However, when an unwary wasp or cricket happens by, the legs unfold at great speed, trapping the prey item in a nearly unbreakable grip between the scimitar-like apical claw of the tibia and the discoidal spines lining the anterior surface of the femur. In addition to the raptorial front legs, the most obvious physical features of mantids are an elongated prothorax and a highly mobile head with which the insect can actually look over its shoulder. Mantids employ accurate binocular vision to assess prey (or enemy) size and distance, and at least some species have an ear that can detect the ultrasound emitted by insectivorous bats hunting the night sky for prey.

Most orthopteroid insects are either herbivores or omnivores, but all mantids are carnivores. Aside from this commonality, mantids are otherwise quite diverse in form and function. There are, for instance, two distinct modes of predation. Most species are sit-and-wait ambush predators such as the leaf mimic, *Phyllocrania illudens,* from Madagascar, the spectacular Malaysian flower mimic, *Hymenopus coronatus*, and the simply cryptic European mantis, *Mantis religiosa*. However, some species are active hunters that run down their prey, such as the North American species, *Yersiniops sophronicum*. Most mantids are winged and sexually dimorphic, but *Brunneria borealis* from the southern U.S.A. is a wingless, completely parthenogenetic female species. In many winged species, only the male has appreciable flight capability; the wings of females often are too small for flight, but can be used in defense (deimatic displays) or to help disperse sex pheromones. Since males cannot by themselves colonize new habitats, the dispersal of mantid populations within a region is generally slow.

Adult body size varies greatly among species; the smallest known species being *Mantoida tenuis* (1 cm) and the largest is *Ischnomantis gigantas* (17 cm). The genetics of sex determination also differs among mantids: males of some species are XO, while many others are XXY.

Life History

Most species of mantids are relatively rare and narrowly distributed in the tropics, an extreme example of which is *Galapagos solitaria*, which is only found on three of the Galapagos Islands. However, some temperate zone species are both abundant and widely distributed. Thus, in spite of the vastly greater diversity of tropical mantids, we know much more about the biology of a few temperate zone species. The best known, most ubiquitous species undoubtedly is the Chinese mantis, *Tenodera aridifolia sinensis*, which occurs throughout much of Eurasia and (through introduction) eastern North America. The life cycle of this species is closely governed by seasonality, typical of many large-bodied, semelparous insects in temperate regions. Egg hatch for the Chinese mantis occurs in the spring, followed by a long maturation period during the summer and sexual maturity early in the fall. Nymphs develop through six or seven instars, during which they may increase from 10 mm to 10 cm in body length. By the time they are adults, males outnumber females by as much as 2:1 (Fig. 106). In the fall, adult females emit pheromones to attract males, and perhaps other females as well. The adaptive utility of the first function is obvious; the latter may be explained as a mechanism to increase the total pheromone concentration in the area of grouped females, resulting in a higher probability that males will be attracted.

After mating, a female deposits one or (infrequently) more oothecae on a stalk of vegetation, each ootheca containing from 60 to 300 eggs, and constituting as much as 50% of the female's pre-oviposition weight, a considerable parental investment at a time when prey are becoming scarce (Fig. 107). The eggs of this and many other species are subject to mortality from parasitoid wasps and, if deposited far enough above the ground, foraging birds.

Praying Mantids (Mantodea), Figure 106 Three male *Tenodera sinensis* competing to mate with the same female. Males typically outnumber females at the beginning of the adult portion of the life cycle, but sexual cannibalism may reduce the discrepancy by the end of the season.

Praying Mantids (Mantodea), Figure 107 Female *Tenodera sinensis* with her ootheca. The egg mass weighs about as much as she does after oviposition.

Adults die with the onset of cold weather, and eggs over-winter. Unlike the European mantis, *Mantis religiosa,* the eggs of which have an obligatory cold diapause, the eggs of the Chinese mantis begin to develop as soon as they are laid, so an extended fall can be lethal if egg hatch occurs before onset of winter. This limits the southern distribution of this species, and extreme cold limits the northern range by desiccating the eggs during winter. Although successive generations of temperate zone species do not overlap, adult females of some tropical species, such as *Cardioptera brachyptera*, live long enough to exhibit parental care by guarding their oothecae and hatchlings against predators.

Mantids in general, and females in particular, are famous cannibals. This trait has led some authors to speculate that a male commits "adaptive suicide" by allowing his mate to consume him, thus contributing to the fitness of his offspring by providing nourishment for egg production. This popular notion is unlikely to be true because females begin to produce their first clutch of eggs before they mate, and the male victim has no assurance of paternity because females may attract and copulate with many males. Furthermore, although sexual cannibalism is frequently observed in the laboratory, under natural conditions males usually escape their first sexual encounter to mate with other females (however, the more mating attempts the greater the probability of being eaten). The simplest explanation for sexual cannibalism is that a very hungry female will eat her suitor before copulation can begin, a mildly hungry female will eat him during or shortly following copulation (if she can catch him), and a female that is less hungry than amorous will let him go. In the first two instances the male does indeed contribute to his mate's nutrition, and therefore to her fitness, but not necessarily to his own because she actually may have been inseminated by a previous male. Considering that females often are food limited at the end of the season and that there are fewer of them than of males, cannibalism of male mantids may be a female's best strategy for producing a healthy ootheca in many instances.

Ecology and Economic Importance

Praying mantids have a tritrophic niche, i.e., they simultaneously occupy two consumer trophic levels in natural ecosystems by virtue of feeding on herbivores, other carnivores and pollen. Mantids, therefore, can compete with other predator species (e.g., spiders) for food, eat other predators, compete with each other, or cannibalize each other. The fact that all of these processes may be occurring at the same time in the same ecosystem can complicate prediction of the impact of these predators on ecosystem structure and dynamics. Predators of mantids include larger spiders and vertebrates such as birds, lizards, and snakes. Other enemies include chalcoid wasps that are parasitic on eggs, and tachinid flies that parasitize nymphs.

Field experiments have shown that mantids exert both direct (prey reduction) and indirect (prey enhancement) effects on arthropod assemblages. Indirect effects occur because competition with, or predation on, other predators may reduce predation on some herbivorous arthropods. An experiment in a complex old-field ecosystem revealed that mantids had a positive effect on plant productivity by reducing herbivorous insects, a direct effect known as a trophic cascade because it ramified two trophic levels down from the predators. However, in another study, mantid nymphs indirectly enhanced aphid densities by reducing spider populations. This kind of unpredictability has important implications for one of the most persistent ideas about mantids, that they are good biological control agents. To that dubious end, oothecae of *Tenodera aridifolia sinensis* are sold and distributed through the mail by organic gardening suppliers. Although this has resulted in much of the broad regional distribution of this species in the U.S., the value of these animals to pest control is dubious at best. Because they are generalists, they eat anything that moves within a suitable size range, and this includes spiders, wasps, bees, butterflies, and other desirable species as well as deleterious herbivores (Fig. 108). In fact, flower-foraging insects such as bees may constitute a significant portion of their diet at the end of the season when grasshoppers and other herbivorous prey are becoming scarce. Thus, planting mantids in one's garden is not necessarily an efficacious way to control pests. There is also a chance that by spreading this exotic species around the country we may be affecting native arthropod assemblages, including native mantid species such as *Stagmomantis carolina*, which often is eaten by the larger Chinese mantid.

Praying Mantids (Mantodea), Figure 108 Adult female *Tenodera sinensis* feeding on a bee. Pollinators such as bees, wasps, and butterflies are frequent prey, especially for adult mantids.

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Precinction

The occurrence of taxonomic groups restricted to, and having originated in, a given geographical region. Most writers use the word endemism to label this condition, but the word endemism is based on the word endemic. The word endemic was first used in ecology in the early 17th century, and has consistently been used in that sense. More than 250 years later, it was misappropriated and used in another sense in biogeography.

► Endemic
► Endemism
► Precinctive

Precinctive

Native to a specified area, and not occurring elsewhere.

► Invasive Pests

Precision

A statistical measure of the repeatability of an estimate relative to a group of estimates from the same population at the same time. Typically measured as the quotient of the standard error of the mean over the mean. Low numerical values indicate high precision, high numerical values indicate low precision. Precision is a key element in developing and evaluating the performance of sampling plans.

► Sampling Arthropods

Preclearance

From a regulatory perspective, this is the certification that in the country of origin, an imported commodity was free of infestation, or produced in a manner that would eliminate risk of infestation. Such commodities are inspected under the supervision of the national plant/animal protection organization of the country of destination.

► Invasive Species
► Regulatory Entomology

Precocenes

Chemical substances from the common bedding plant *Ageratum houstonianum* that affect the development of some insects by causing atrophy of the corpora allata and causing precocious maturity and production of sterile adults.

Predaceous (Predacious)

Animals that attack and feed upon (prey upon) other animals. Ecologists sometimes consider consumption of plants by animals to be predation, but entomologists call such animals herbivores and this process herbivory.

Predaceous Diving Beetles

Members of the family Dytiscidae (order Coleoptera).

► Beetles

Predation: The Role of Generalist Predators in Biodiversity and Biological Control

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The term "generalist predator" is nearly redundant. The diets of the vast majority of predators are far less specialized than many herbivore-plant associations in which, for example, the life cycle of a phloem-feeding treehopper (Hemiptera: Membracidae) in the temperate zone may be completely dependent on the seasonal phenology of a single species of tree. Although some groups such as ladybird beetles (Coleoptera: Coccinellidae) are relatively specialized on a few related prey species (in this case, mainly aphids or scale insects), the vast majority of predators feed on varied prey. A far more typical group of coleopteran predators, beetles in the family Carabidae, will take nearly anything that moves within a size range they can physically handle, regardless of taxonomic position. Thus, the most important factor determining the niche (ecological role) of insect predators undoubtedly is breadth of diet.

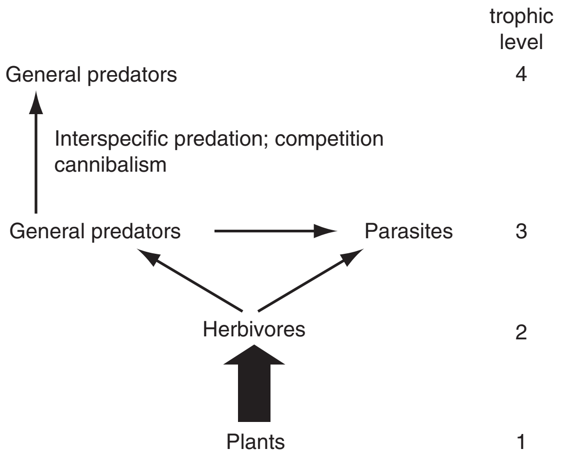
The Niche of Generalist Predators

Predatory insects are fewer in number than herbivores owing to the constraints of the second law of thermodynamics, which dictates that the energy available to higher trophic levels in a food chain diminishes with each transfer. This is why food chains often are represented as pyramids, getting smaller from the ground floor (plants), through the consumer levels, with top carnivores occupying the narrow tip. Most predators are probably generalists because carnivores that feed broadly can sustain larger populations than those specializing on one or a few prey species. A specialist will starve if its prey population gets too low, but a generalist can sustain its population size on alternate prey even if preferred prey species become scarce (see functional response, below). This is a key tenet of niche theory: resource generalists are more buffered against fluctuation in those resources than are specialists.

A voluminous literature suggests that phytophagous insects do not often compete, i.e., are not routinely food limited, whereas most studies that have addressed the question have found that predators usually are limited by their prey. In spite of this apparent thermodynamic disadvantage of the predatory lifestyle, feeding on animal prey does provide one potential advantage over vegetarian fare: higher quality protein. There are even many examples in the animal kingdom of predominately herbivorous animals that are carnivorous as juveniles (when growth is important) or as adults during reproduction (for egg production). After all, adult female mosquitoes (Diptera: Culicidae) feed on blood to make eggs.

Most major insect orders have predaceous members. These may be dedicated carnivores such as dragonflies and damselflies (Odonata), mantids (Dictyoptera), ambush bugs (Hemiptera), and lacewings (Neuroptera), or they may be omnivores such as ants (Hymenoptera), earwigs (Dermaptera), and crickets (Orthoptera). The manner of predation also varies widely: carabid beetles (Coleoptera) chew their victims, while reduviid bugs (Hemiptera) suck them dry as do spiders; water scorpions (Hemiptera) and some mantids, like orb weaving spiders, are sit-and-wait ambush predators, while wasps (Hymenoptera) tend to be active hunters. Some, such as the aquatic naiads of Odonata, will even include vertebrates in their diets. These predators, and others such as diving beetles (family Dytiscidae) and giant water bugs (family Belostomatidae) are particularly adept at capturing small fish and tadpoles.

The amount of research on predatory insects is far exceeded by work on herbivores, for the obvious reason that most insect pests are herbivorous. For that reason, we know much more about plant feeders than about the insects that eat them. Our growing awareness of the environmental hazards of biocide use has contributed to research on some



Predation: The Role of Generalist Predators in Biodiversity and Biological Control, Figure 109 **The trophic position of generalist predators is complicated by the varied interactions that can take place among them, as well as by their relationship with the rest of the community. Arrows represent direction and relative amount (line thickness) of energy flow in food webs topped by general arthropod predators, illustrating their bitrophic position as members of both the third and fourth trophic levels.**

predatory species to investigate their potential for biological pest control. However, we still have much to learn about how predators fit into complex natural communities.

The Predator Guild and Community Interactions

A guild is a group of species that use a common resource base. A community of organisms within a habitat generally comprises many guilds using many different, sometimes overlapping, resources. Guilds often consist of species that are not particularly closely related, but that have overlapping resource requirements. Thus, a guild of predatory animals that feed on ground-dwelling arthropods may consist of such invertebrates as wolf spiders, scorpions and tiger beetles, along with vertebrates such as lizards and shrews (Fig. 109).

Generalist arthropod predators typically are bitrophic: they simultaneously occupy the third and fourth trophic levels by virtue of feeding both on herbivores and on each other. As a consequence, species within generalist predator guilds may compete with each other for common prey resources, or they may eat each other. Predation can be either between species or among individuals within the same species, because most generalist predators are cannibals. In fact, cannibalism often has been proposed as a mechanism of population regulation in such predators because the frequency of cannibalism is expected to increase as population density increases, resulting in negative feedback between population size and cannibalism. The selective advantage of cannibalism is simply that a cannibalistic individual can increase its Darwinian fitness by eating members of its own cohort when alternate prey are scarce. The combination of cannibalism and interspecific predation within predator guilds has become known as intraguild predation.

The combination of competition, interspecific predation, and cannibalism not only influences coexistence within this guild, it also complicates the impact of these predators on the rest of the community. Both competition for scarce prey and intraguild predation can occur even among predators of different phyla (e.g., between amphibian larvae and aquatic insects). There is yet another wrinkle in the food web. It has been suggested that predators be thought of as mutualists of plants, because plants supply them herbivore prey and they in turn reduce damage from herbivory. However, predators such as ambush bugs and crab spiders can be viewed as competitors with plants for a common resource: pollinating insects such as bees and butterflies.

In view of the complex relationship of generalist predators to each other and to the rest of the community, it is not surprising that we do not yet have good predictive models of their impact on diverse insect assemblages. Finding out how generalist predators affect highly diverse natural communities requires careful experimentation in the field, in which predators are either eliminated or their densities augmented in replicated plots, and the results are compared with control plots with normal predator levels. These experiments usually are difficult to perform, and the resultant data (usually in the form of changes in numbers of individuals or biomass among resident species) are nearly always highly variable, necessitating relatively complex statistical analysis. For these reasons, such experiments are not as common in the literature as are laboratory tests of predator feeding, or experiments using low diversity agricultural plots.

Interpretation of the results of experimental predator manipulations on a target community often can be difficult. When a target (prey) population declines, the cause is usually a direct effect of predation. However, frequently predators actually increase populations of prey species, an indirect effect of their feeding on competitors or on other predators of these prey. In a diverse species assemblage, both kinds of results often occur in the same experiment. The potential combinations of positive and negative effects on prey may even serve to cancel out the overall impact of predators on prey assemblages. Our current understanding of these interactions is still too limited to make reliable predictions of which of these effects will be important prior to adding predators to arthropod assemblages. Clearly, more research is needed.

If predators affect herbivore populations, they may as a result affect the plants on which these herbivores feed. This kind of "top down" effect of predators on successively lower trophic levels is one kind of what is known as a trophic cascade. The other kind, "bottom up," is when plants are demonstrated to control herbivores (rather than the reverse), and herbivores in turn control predators. Trophic cascades are the subject of a growing literature among theoreticians and experimentalists in ecology, and people involved in biological control are obviously interested in the potential for predators to exert top down control. Unfortunately, there are as yet few experiments in the field demonstrating that arthropod predators can exert top down control. One experiment in a simplified agricultural system showed that spiders could boost plant productivity by reducing herbivores; another experiment demonstrated the same sort of effect for praying mantids in a complex natural community. This may seem promising, but before we can make any kind of general prediction, we need many more studies under various conditions.

Generalist Predators and Biological Control

There are some good examples of biological control of pest species using specialized predators, e.g., the control of scale insects on California citrus by the introduction of the Australian ladybird beetle, *Rodolia cardinalis*. Some evidence suggests that at least some arthropod generalists, such as mites and spiders, can significantly reduce herbivore populations in simplified experimental agricultural system, but very few data have been generated as to the effects of this predation on plants. It is therefore reasonable to ask whether generalist insect predators may be useful in the control of those herbivorous and parasitic species that have exceeded the human economic and nuisance threshold: pests.

Pest species are virtually defined as populations that are out of control, and in order to control a pest population, a predator must track its prey closely. This generally requires two kinds of reactions to changes in the size of a prey population by a predator: numerical and functional responses. Numerical response simply means that a predator can adjust its population size to exploit changes in the prey population. The two ways to do this are through increased reproductive output, and high rates of dispersal into areas of high prey density (and, conversely, reduced reproduction and emigration when prey become scarce, to avoid complete starvation). Both of these mechanisms would entail a time lag in predator response, even if the predator were a specialist; this time lag would likely be much longer for a generalized predator.

Functional response is an increase in per capita feeding rate as prey become more abundant. Ideally, a predator should "switch" from generalized feeding on many prey species to focus on the rapidly increasing pest population in a frequency-dependent manner. This entails recognition of specific chemical, tactile, or visual cues provided by the pest species from among all the other prey signals in the environment at the time. This would seem unlikely for a generalist predator, an animal adapted to hunting or ambushing a variety of prey species in a food-limited environment, but even an omnivore may have preference for a specific item from among its dietary choices. The criteria for prey preference in predators vary, but include such factors as ease of capture and nutritional value. The net gain to the predator for an item of prey, when costs of finding and capturing prey are balanced against nutritive gain, are included in the theoretical construct known as optimal foraging theory. This theory predicts that selection will favor those (optimal) behaviors that maximize net return on an animal's foraging expenditure. However, even if a predator did switch to increase its feeding rate on a specific pest, it would reach a satiation level past which further increases in prey density could elicit no faster capture rate per individual predator. Unless this functional response were accompanied by a good numerical response, it would be unlikely to work.

The general unpredictability of community-wide effects of adding predators to experimental systems discussed in the previous section argues against their use in the absence of careful prior study. A predator may feed broadly enough that its diet encompasses a pest species, but once introduced it may exhibit preference for other prey, either benign or beneficial. The fact is that generalist predators may eat as many or more beneficial species as they do pests, and the tradeoff between positive and negative effects of these predators in our gardens can make them unreliable biocontrol agents.

Value of Predators to Biodiversity

It is becoming increasingly obvious that predators of all kinds play a critical role in the maintenance of biodiversity. So, to the extent that humans are concerned with the variety of life forms in nature, we should pay attention to the carnivores. Human history is rife with examples of human extirpation of vertebrate carnivores, as we have spread ourselves across the habitable world. This has happened largely because tigers, wolves, rattlesnakes, and hawks have been perceived to compete with us for what we eat (including domesticated animals), or are feared because they can harm us. As a result, we have a superabundance of animals like deer, rabbits, rats, and groundhogs, but a general decline in biological diversity in proximity to human settlements.

Among arthropods, predators have been implicated as important selective agents in the evolution of herbivore-plant systems. Evidence of strong natural selection exerted by predators includes the numerous examples of adaptations among herbivorous insects to detect and avoid them. This includes remote sensing to chemically identify the whereabouts of an enemy, clearly a case for considerable evolutionary fine-tuning of a prey to its predator. It seems quite likely that predators play an important role in controlling the diversity of the arthropod portion of the biosphere. This is a large slice of life indeed, considering that about 64% of all species identified so far are insects, so it would not be surprising if much of the rest of global biodiversity depended on them as well.

Adding exotic predators to control pest species may have the undesirable effect of decreasing native insect diversity. Some studies have suggested that introduced predators can interfere with native species, resulting in loss of control over prey populations through release from predation, i.e., making a bad situation worse in terms of levels of pest populations. Or, an introduced predator may simply displace, through competition or intraguild predation, a native predator. An example of this is the Chinese praying mantis, *Tenodera sinensis*, introduced into the United States a little more than 100 years ago. This species has not only become the most abundant and widespread mantid in this country (mainly by human transport of egg cases), it has displaced one of our native species, the Carolina mantid, *Stagmomantis carolina*, from some habitats in North Carolina. In this case, the mechanism is predation: both species lay their eggs on loblolly pines, but the Chinese mantid is larger and finds the Carolina mantid easy prey. It is therefore uncommon to find both species persisting in the same habitat for very long.

Whatever their effects, once introduced insects can be very hard to remove from their adopted home. In archipelagos such as Hawaii and the Galápagos, where entomologists have been keeping score, the proportion of exotic insects making up the species list has been growing at an alarming rate ever since these islands were colonized. Most biologists recognize diet breadth as one indication of how likely an animal is to be invasive. The very fact of their broad diet can make generalist predators ideal invasive species, preadapted for survival in novel habitats with a naive (unadapted) prey assemblage. Given that species invasions are second only to habitat loss as a threat to global biological diversity, and that uncountable introductions have been made inadvertently through global human travel and commerce, we certainly must be especially careful about introducing insects intentionally.

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Predator

In entomology, animals that feed on insects, and must eat several or many insects in order to complete their life cycle.

Predatory Guild

A group of different types of organisms that feed on the same resource, such as a developmental stage of an insect.

Predatory Stink Bugs (Hemiptera: Pentatomidae, Asopinae)

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The subfamily Asopinae belongs to the family Pentatomidae of the suborder Heteroptera (true bugs). About 300 species in 69 genera have been described worldwide.

- Order: Hemiptera
  - Suborder: Heteroptera
    - Infraorder: Pentatomomorpha
      - Superfamily: Pentatomoidea
        - Family: Pentatomidae
          - Subfamily: Asopinae

External Morphology

Like other Pentatomidae, predatory stink bugs or soldier bugs are of moderate to large size, ranging in length from 7 to 25 mm, and are broadly elliptical in shape. The piercing-sucking mouthparts of predatory stink bugs consist of a four-segmented rostrum or beak (labium) forming a sheath that encloses two mandibular and two maxillary stylets. Whereas the rostrum of phytophagous pentatomids is slender, asopines are characterized by having a thickened rostrum.

In asopines, the first segment of the rostrum is markedly thickened and free, which enables the rostrum to swing forward fully, making it easier for the predator to feed on active prey. The appearance of the rostrum can be a useful diagnostic character for distinguishing the beneficial predatory pentatomids from potentially harmful phytophagous pentatomids in the field. The triangular mesothoracic shield, called the scutellum, is usually much shorter than the abdomen, but in some genera it is enlarged, covering most of the abdominal dorsum. The males of Asopinae are unique in combining the presence of genital plates with a thecal shield. The shape of the male claspers or parameres is the most reliable diagnostic characteristic for the identification of species.

Habitat and Food

Predatory stink bugs are found in a wide range of natural and agricultural habitats, but many species appear to prefer shrubland and woods. The Asopinae are set apart from the other pentatomid subfamilies by their essentially predaceous feeding habits. It is believed that the Pentatomomorpha have arisen as plant feeders and that only the subfamily Asopinae has secondarily become predaceous. First instars do not attack prey and only need moisture, mainly in the form of plant juices, to develop. Although, for some species, partial development on certain plant-based diets has been reported, nymphs from the second instar on require animal-based diets to complete development. Nymphs and adults, however, are often observed to take up plant juices or free water in addition to feeding on animal prey. Plant feeding primarily provides moisture, but it may also furnish certain nutrients to the bugs. This habit may help predatory stink bugs to sustain their populations in times of prey scarcity. In contrast to some other zoophytophagous heteropterans, plant-feeding asopines have not been reported to injure plants.

Predatory stink bugs attack mainly slow-moving, soft-bodied insects, primarily larval forms of the Lepidoptera, Coleoptera and Hymenoptera. Very few, if any, Asopinae are truly host-specific. Nevertheless, whereas some asopine bugs are generalist predators, attacking a wide array of prey in a diversity of habitats, others appear to be more closely associated with a limited number of insect species and occur in only a few habitats. It has been hypothesized that there may be an evolutionary progression from the drab asopines, which feed rather generally, to the brightly colored asopines, which prefer larvae of Chrysomelidae and, to a lesser extent, Coccinellidae.

Life History

The eggs are usually laid in masses. In some species (e.g., *Podisus*), the eggs bear prominent micropylar processes. There are five nymphal instars. The nymphs take a few weeks to develop, depending on temperature and food. Newly emerged nymphs are highly gregarious, whereas later instars become progressively more solitary with each molt. First instars are not predaceous and take up only water or plant juices; occasionally, they also feed on unhatched eggs. From the second instar on, nymphs begin searching for prey shortly after molting. The nymphs will feed up to 1–2 days before the next molt; at that time, their activity drops and the nymphs will remain resting in a concealed place in preparation for the oncoming molt. Small nymphs tend to attack prey and feed collectively, particularly when the prey is large. Larger nymphs and adults prefer to attack prey individually. Under conditions of food shortage, the nymphs and the adults are highly cannibalistic. The adults are long-lived, with reported longevities of 15 days to more than 3 months, and they lay eggs throughout their entire lifetime. The adults usually move by crawling, but some species (including *Podisus maculiventris*) are also noted to be good flyers. Field surveys suggest that scelionid egg parasitoids, such as *Trissolcus* and *Telenomus* spp., are the most important natural enemies of predatory stink bugs.

Prey Location and Capture

Predatory stink bugs use visual, chemical and tactile cues to locate and recognize their prey. Vision appears to be the most important sense used by the bugs to locate prey. *Podisus maculiventris* and other asopine bugs react to moving prey at distances up to 10 cm, but their reactive distance to immobile prey is considerably less and detection often seems to occur at antennal or rostral contact. Evidence is accumulating that several asopines can also use airborne chemical cues for prey detection. Both *Podisus maculiventris* and *Perillus bioculatus* are sensitive to systemic volatiles produced by plants in response to prey feeding. *Eocanthecona furcellata* is attracted to its lepidopterous prey based, in part, on a volatile component derived from the chlorophyll ingested by the prey. Further, it has been demonstrated that *Podisus maculiventris* can use vibrations of the substrate as cues for prey location. Prey recognition is based primarily on antennal and rostral contact. Asopines are rather timid predators. After finding the prey and orienting to it, the bugs may spend from several minutes up to an hour stealthily approaching it, often keeping their beak extended forward. The stylets are usually inserted at soft areas of the prey body. During attacking and feeding, the only contact between predator and prey is by the rostrum and stylets. When stylet penetration is perceived by the prey, many prey species will try to escape by vigorous body movements. The harpoonlike structure of the mandibular stylets enables a tenacious hold on the prey during this struggle. Further, predatory pentatomids are presumed to inject a salivary toxin into the prey body that quickly immobilizes it. During feeding, body tissues of the prey are liquefied by the injection of digestive enzymes and by the lacerating action of the stylets. The liquid and partly digested food can then be sucked up through the rostrum. This "solid-to-liquid" feeding process enables the predator to use most of the body tissues of the prey.

Pheromones

Both male and female asopines possess a metathoracic scent gland from which they discharge a disagreeable odor when disturbed, hence the name "stink bugs." In addition, many species of predatory stink bugs have discrete pheromone glands, which belong to one of two types: dorsal abdominal glands (in both sexes) or sternal glands (in males only). Species with dorsal abdominal glands are mostly polyphagous predators (e.g., *Podisus*, *Zicrona*), whereas those with sternal glands often appear to be more specialized predators (e.g., *Perillus*, *Stiretrus*).

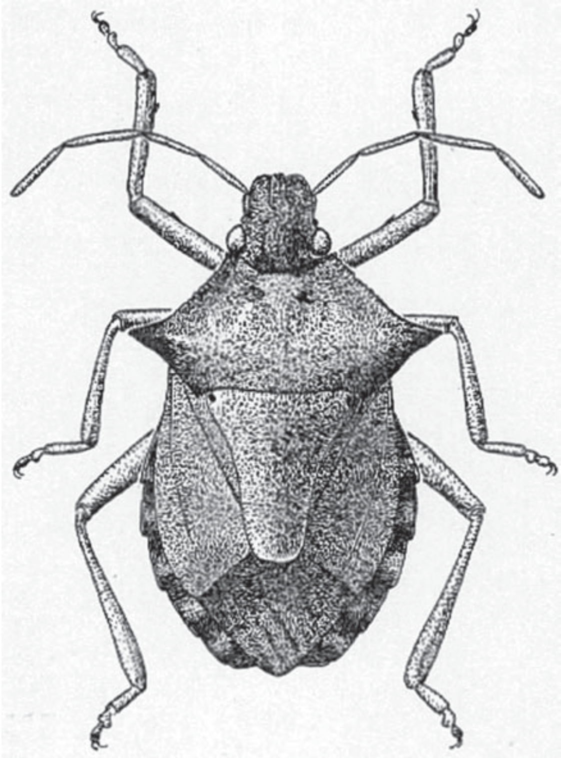
The best known pheromone system is that of the spined soldier bug, *Podisus maculiventris*. Adult males of this species possess hypertrophied dorsal abdominal glands that produce secretions that function as long-range attractants for adults and immatures of both sexes. Immature predators are thought to use the male pheromone as a cue indicating the presence of prey. In the United States, attractors with a synthetic pheromone are commercially available to lure spined soldier bugs to target areas in early spring when the adults emerge from overwintering. Pheromone-baited traps can also be employed to capture large numbers of predators that can be used to establish mass cultures.

Economic Importance

Several predatory pentatomids are believed to have a future for the biological control of various economically important crop pests in different parts of the world. To date, however, the only asopine that has been commercially available for augmentative biological control in North America and Europe is the spined soldier bug, *Podisus* *maculiventris*. This species is native to North America and has shown good capacity to control a variety of insect pests in field and greenhouse crops, orchards and forests, including the Colorado potato beetle, *Leptinotarsa decemlineata*, and several leaf-feeding caterpillars. The two-spotted stink bug, *Perillus bioculatus*, is another important natural enemy of the Colorado potato beetle in North America. *Podisus nigrispinus* is the most common predatory stink bug in South America. The insect has been the subject of conservation and augmentation biological control programs against leaf-feeding caterpillars in forests, including Eucalyptus stands in Brazil. In Southeast Asia and India, *Eocanthecona furcellata* has received increasing attention for its potential to control outbreaks of lepidopterous and coleopterous defoliators. *Picromerus bidens* (Fig. 110) was originally a widely distributed Palearctic species, but it has been found in the northeastern United States and eastern Canada since its (accidental) introduction sometime before 1932. Although its biology has been studied to some extent, few studies have attempted to quantify its predatory effectiveness. Given that only 10% of the nearly 300 known species of Asopinae has been studied in more or less detail, obviously an enormous biocontrol potential remains to be investigated.

► Stink Bugs (Hemiptera: Pentatomidae) Emphasizing Economic Importance

► Bugs (Hemiptera)



Predatory Stink Bugs (Hemiptera: Pentatomidae, Asopinae), Figure 110 **Line drawing: *Picromerus bidens* (taken from T.J. Henry and R.C. Froeschner, 1988. Catalog of the Heteroptera, or True Bugs of Canada and the Continental United States. E.J. Brill).**

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Predisposing Factors

Factors which, by their actions, render an organism susceptible to a certain disease; conferring a tendency to disease.

Pre-Emergence Treatment

Treatment of a plant, usually with a pesticide, before the plant has emerged from the soil.

Pre-Planting Treatment

Reference to a treatment applied to a crop before planting.

Prepupa

A generally quiescent, occasionally active but non-feeding, stage of insects at the end of the immature development period. The period immediately preceding the molt to the adult stage. In thrips, it is the third instar.

Prescutum

The anterior portion of the meso- and metanotum.

► Thorax of Hexapods

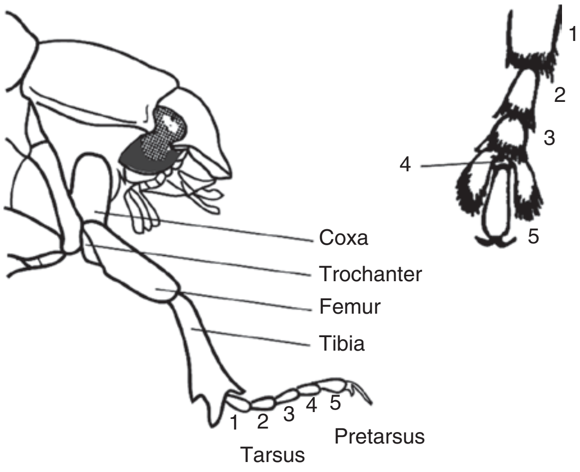
Presocial Behavior

Expression of one or two (but not all three) of the following traits of sociality: individuals of the same species cooperate in caring for the young; there is division of reproductive behavior, with more or less sterile individuals working on behalf of the fecund individuals; overlap of at least two generations in life stages contributing to colony labor, so that offspring can assist parents during some period of their life. Thus, presocial behavior is considered to include all the stages intermediate between solitary and eusocial behavior.

► Subsocial
► Communal
► Quasisocial
► Semisocial
► Eusocial Behavior

Prevalence

The frequency of occurrence. In ecology, the proportion of inhabitable sites or areas inhabited by an organism. With respect to epizootiology, the total number of cases of a particular disease at a given moment of time, in a given population.



Pretarsus, Figure 111 **Leg of a beetle (Coleoptera: Scarabaeidae) leg showing its component parts, and a close-up of one type of beetle tarsus (foot).**

Pretarsus

The terminal portion of the leg. The tarsal claws and associated structures (Fig. 111).

► Legs of Hexapods

Prey

In entomology, insects that are eaten by predatory animals (including other insects). If the insect is killed by a parasitoid or pathogen, the insect is called a host, not the prey.

Primary Parasitoid

A parasitoid of a host, not of another parasitoid.

Primary Production

Production by green plants (contrast with secondary production).

Primary Productivity

The rate at which biomass is produced by plants, expressed on a per unit area basis.

Primary Reproductives

In social insects, the pair of insects that founds the colony.

Primer

In molecular biology, a short oligonucleotide that is attached to a ssDNA molecule in order to provide a site at which DNA replication can begin.

Primer Pheromone

A pheromone that acts to modify the physiological condition of an animal (contrast with releaser pheromone).

Primitive Caddisflies

Members of the family Rhyacophilidae (order Trichoptera).
► Caddisflies

Primitive Carrion Beetles

Members of the family Agyrtidae (order Coleoptera).
► Beetles

Primitive Crane Flies

Members of the family Tanyderidae (order Diptera).
► Flies

Primitive Dampwood Termites

Members of the termite family Termopsidae.
► Termites

Primitive Weevils

Members of the family Belidae (order Coleoptera).
► Beetles

Prionoglaridae

A family of psocids (order Psocoptera).
► Bark-Lice, Book-Lice or Psocids

Probability Model

In sampling, a mathematical description of the dispersion or distribution of individuals in a population based on numbers per sample unit. Common models include Poisson, Negative-binomial, Binomial, Normal, and Neyman Type A. Such models can form the foundation of a sampling plan.
► Sampling Arthropods

Probe

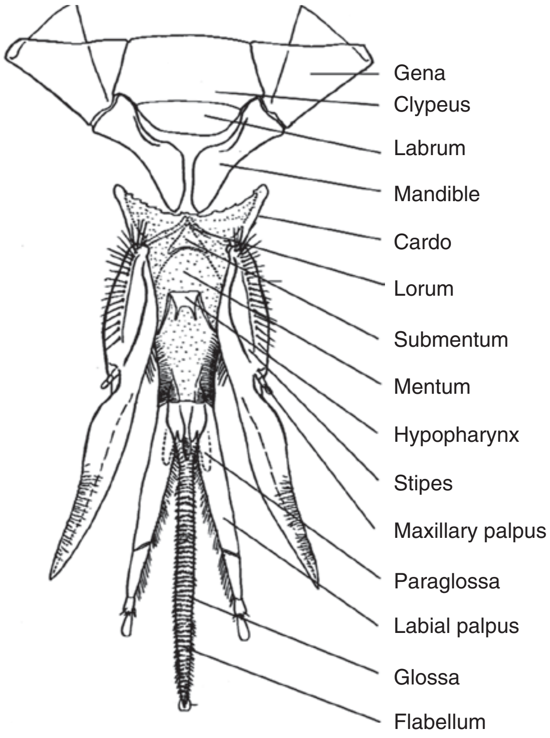
A probe is a molecule labeled with radioactive isotopes or another tag that is used to identify or isolate a gene, gene product, or protein.

Proboscis

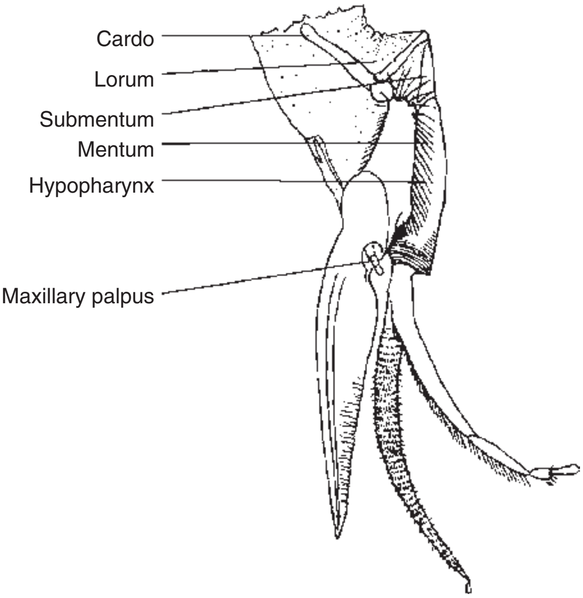
The tube-like or beak-like mouthparts or sucking apparatus of insects that are modified to feed on liquid food (Figs. 112–114).

Process

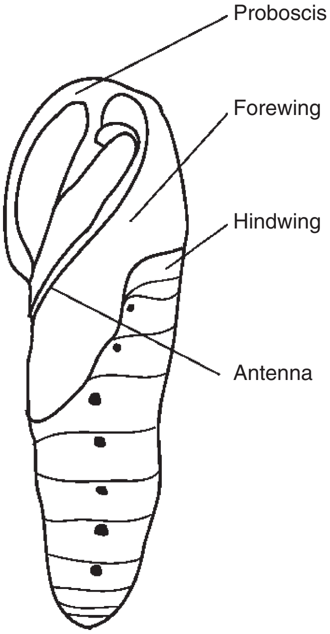
Any projection or prominent part of the body that projects from the surface, but that does not warrant a specific name; examples include bumps, warts, and tubercles.



Proboscis, Figure 112 **Anterior aspect of a proboscis (Diptera).**



Proboscis, Figure 113 **Left lateral aspect of a proboscis (Diptera).**



Proboscis, Figure 114 **Side view of a moth pupa (Lepidoptera: Sphingidae) showing the proboscis.**

Proctodeum

The hindgut of insects.

► Alimentary Canal and Digestion

Proctotrupidae

A family of wasps (order Hymenoptera).

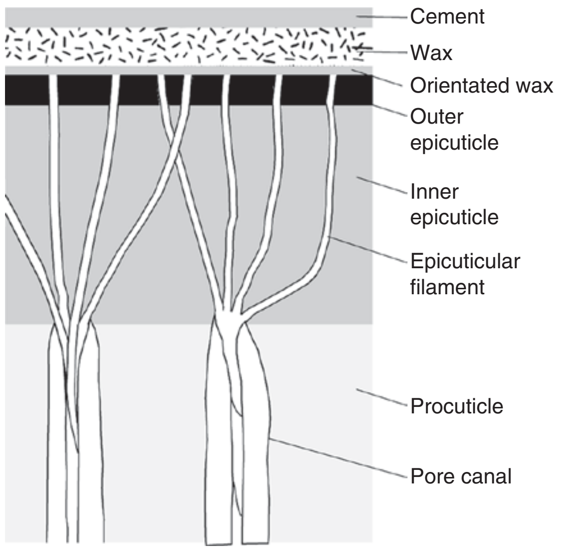
► Wasps, Ants, Bees and Sawflies

Procuticle

The inner zone of the cuticle, divisible into the hard, outer, dark exocuticle and the soft, inner, light endocuticle, and containing primarily chitin and protein. The procuticle exists during molting, before the inner layers of the cuticle (exocuticle and endocuticle) are sclerotized into distinct layers, but this is a temporary condition (Fig. 115).

► Cuticle

► Epicuticle



Procuticle, Figure 115 **Cross section of the insect epicuticle (adapted from Chapman, The insects: structure and function).**

Prodoxidae

A family of moths (order Lepidoptera). They commonly are known as yucca moths.

► Yucca Moths

► Butterflies and Moths

Profitability Concept

The concept that predators will seek prey that provide the most calories or biomass, as this represent the "most profitable" investment of their time by maximizing growth and reproduction. This can also be called optimal foraging.

Prognathous

A condition in which the head is horizontal and the mouthparts are directed forward. This is particularly common in burrowing and predatory species.

► Mouthparts of Insects

Progressive Provisioning

Among social insects, the act of provisioning the larva at intervals during its development, as opposed to mass provisioning.

Prohemocyte

Very small hemocytes, possibly giving rise to other types of hemocytes.

► Hemocytes of Insects: Their Morphology and Function

Projapygidae

A family of diplurans (order Diplura).

► Diplurans

Prokaryote

An organism whose cells lack a distinct nucleus.

Prokopy, Ronald J

Ron Prokopy was known for innovative and insightful research on insect behavior that led to new approaches to effective pest management. He was born September 28, 1935 in Danbury, Connecticut, USA. He was raised on the family apple farm, an experience that likely explains his life-long fascination with apple pest management in general, and apple maggot in particular. After earning a B.S. and Ph.D. degree from Cornell University in 1964, Prokopy joined the Connecticut Agricultural Experiment Station, working on apple pests. There he was influenced by Jim Kring, who was studying host location by flying aphids. Prokopy initiated study of the visual orientation of apple maggot flies, examining how shape, color, and size of fruit and foliage influence fly behavior. A trademark of Prokopy's work then, and throughout his career, was the direct observation of these day-active insects. He manipulated the insects or their environment, either in cages or in the field, then watched and recorded their unusual and unanticipated actions for hours.

Prokopy traveled to Europe beginning in 1968, working in Poland, Switzerland, and Greece, but also worked with Guy Bush in Texas before settling into the "Prokopy Bio-Experimental Farm in Wisconsin." In 1975, he joined the University of Massachusetts, where he conducted research and educational programs for apple growers, and taught a course in insect pest management. His mission while in Massachusetts was to reduce or eliminate insecticides, a tall order for an industry grown accustomed to blemish-free fruit. Unlike most extensionists, Prokopy eschewed presentations about new and more effective insecticides, focusing on insect behavior. Perhaps because he had his own commercial orchard, growers listened to his advice, and gradually insecticide use was reduced. But Prokopy's personal intensity, knowledge, and integrity also contributed to his success in changing the attitudes and actions of growers, and they were soon great supporters of his philosophy. This high level of commitment, and a seemingly unending supply of energy, made him a popular mentor and collaborator.

Prokopy was a popular speaker and a prolific author. He published about 275 journal articles during his career, and over 400 scientific publications in total. He pioneered research on apple maggot fruit marking pheromone, and on using red, spherical sticky traps for population monitoring and removal trapping. Prokopy received many honors and awards. From the Entomological Society of America he received the Distinguished Service Award in Extension, founder's Memorial Award, Buzzard Award, and was named a Fellow of the Society. He also received a Guggenheim Fellowship, and a Fulbright Fellowship, and received both research and extension awards from the University of Massachusetts. Ron Prokopy died on May 14, 2004 in Greenfield, Massachusetts.

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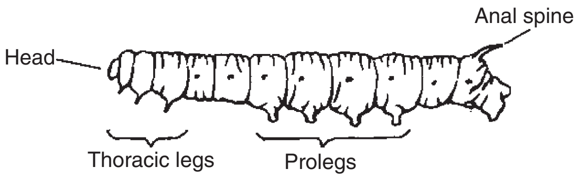

Proleg, Figure 116 **Lateral view of a "hornworm" caterpillar (Lepidoptera: Sphingidae).**

Prolarvae

Newly hatched larvae without completely functional legs, and incompletely sclerotized integument. Such larvae often remain aggregated.

Proleg

A fleshy, unsegmented appendage serving as a leg and found on the abdomen of some holometabolous insects, particularly caterpillars and sawflies (Fig. 116).

Prominence

A section of the body that is raised, elevated, or projecting.

Prominent Moths (Lepidoptera: Notodontidae)

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Prominent moths, family Notodontidae (including processionary moths), total 3,562 species from all faunal regions, most from the Neotropics (1,766 sp.); actual world fauna likely exceeds 4,000 species. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. The subfamily classification varies, but currently involves eight subfamilies, with segregation into three groups: Oenosandrinina (for Oenosandrinae, with three species in Australia), Thaumetopoeinina (for Thaumetopoeinae, and Notodontinina (for the remaining six subfamilies). Dioptidae (including Doinae) are sometimes included in Notodontidae. Adults small to very large (20–124 mm wingspan); some with massive bodies. Maculation varied, but many with subdued browns and grays; some white and a few more colorful or with iridescent markings. Adults mostly nocturnal. Larvae are leaf feeders, sometimes gregarious (especially among Thaumetopoeinae) and feeding nocturnally. Host plants include a large variety of plant families, especially for broadleaf forest trees. A number of economic species are known, especially among the processionary caterpillars (subfamily Thaumetopoeoinae) (Fig. 117).

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Prominent Moths (Lepidoptera: Notodontidae), Figure 117 **Example of prominent moths (Notodontidae), *Epicoma melanosticta* Donovan from Australia.**

Promoter

A region of DNA crucial to the accuracy and rate of transcription initiation. Usually immediately upstream of the gene itself.

Pronotal Comb

In fleas, a row of strong spines on the posterior margin of the pronotum.

Pronotum

The upper or dorsal surface of the prothorax, often shield-like in form.

► Thorax of Hexapods

Pronunciation of Scientific Names and Terms

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Many words of Greek and Latin origin are used in entomology and are of two kinds. The first kind is words that have been adopted into English and other modern languages to describe forms, structures and processes. The second kind is the Latin (scientific) names of taxa at all classificatory levels. Their pronunciation has caused confusion.

Once, Latin was a living language. For many hundreds of years after the fall of Rome, Latin was the common language in western Europe, a means by which educated people in various countries communicated. That is why Linnaeus in the eighteenth century wrote his Systema Naturae in Latin rather than in his native Swedish. It is why Latin was used for binominal nomenclature. Later, French and then English became widely used, and the editions of the International Code of Zoological Nomenclature are written in those two languages although the names of taxa are still nominally Latin and follow the rules of Latin grammar.

Even by the time of Linnaeus, Latin pronunciation had diverged from country to country in western Europe to acquire the characteristics of each native language. By the late nineteenth century, Latin as pronounced in England (and, by extension, also in the USA, Australia, Canada, and New Zealand) had acquired the vowel and diphthong sounds of English, whereas Latin as pronounced in France had acquired some peculiarities of French. Likewise in Germany and Italy. Although Latin was written identically in countries of western Europe, it no longer was pronounced the same. In recognition of this problem, Latin scholars met to reconstruct pronunciation of Roman Latin, and then to begin its teaching in the early decades of the twentieth century. By the mid twentieth century, Latin pronunciation as taught in Latin classes in England, the USA, other English-speaking countries, and countries of continental Europe was once again (more or less) uniform. So we may talk about two systems of Latin pronunciation: corrupted Latin as used in the nineteenth century in English (and differently in other modern languages), and restored Latin as now taught in Latin classes.

But, damage of two forms already had been done. First, many Latin words had been adopted into English and the corrupted form had become the norm in English, as shown for a few words below (Table 17).

Pronunciation of Scientific Names and Terms, Table 17 **Examples of correct (restored) and corrupted English pronunciation of Latin**

Latin word	Restored Latin pronunciation	Corrupted English pronunciation
Alumnae	alumn.eye	alumn.ee
Alumni	alumn.ee	alumn.eye
Larvae	lar.why	lar.vee
Pupae	poop.eye	pyoo.pee

This corrupted English pronunciation is broadly used in biology, medicine and law, and is now engrained in English. We have to accept that such words are English, adopted from Latin, spelled as in Latin, but not pronounced as Latin is now taught. After all, English has adopted and mispronounced many words from other foreign languages. The words beau, bouquet, boutique, lieutenant and lingerie have been adopted from French. They are now used in France, are not relics of a long-defunct language, but yet are commonly mispronounced by English-speakers. The same kinds of changes have befallen other modern languages. French and Spanish too, despite regulation by academies designed to preserve their purity, have adopted, corrupted and mispronounced words from other languages, including English. They have likewise adopted words from Latin, and changed not only their pronunciation but also their spelling.

The International Code of Zoological Nomenclature specifies how scientific names of animals are to be formed. But it does not specify how they should be pronounced.

The most widely used basic entomology textbook in the USA (Borror et al., 1989) provides a few pages about construction of names of scientific names of insects. This explanation for the most part is good and useful. However, as to sounds of vowels, consonants, and diphthongs, it explains only the corrupted English pronunciation as taught in Latin classes in the USA in the nineteenth century. Its instructions are thus out of line with the way that Latin has been taught for the last 50 years. It promotes an outdated system that makes the pronunciation very hard to understand by anyone who learned Latin and/or pronunciation of scientific names in non-English-speaking countries. Generations of entomologists have relied upon this textbook to explain the latest classification of insects,

Pronunciation of Scientific Names and Terms, Table 18 **Pronunciation of Latin vowels, consonants, and diphthongs as now taught in Latin classes**

Vowels	Consonants
a (short) as in apple	b (as in English)
a (long) as in father	c as in cat
e (short) as in get	ch as English k (or k-h)
e (long) as in they	d (as in English)
i (short) as in pit	f (as in English)
i (long) as in machine	g as in go
o (short) as in not	h as in hence
o (long) as in note	i (consonant i [= j]) as y in yes
u (short) as in full	k (as in English)
u (long) as in brute	l (as in English)
y as "ew" but without any trace of y sound	m as in man n (as in English)
	ph as English p (or p-h)
Diphthongs	q as in quite
ae as y in English try	r always rolled
au as ou in English house	s as in sister
ei as in English rein	t as in tanned
eu as "ay-oo" (stress the "ay")	th as English t
oe as oi in English foil	v as English w
ui as in English we	x as in six
	z as in zero

most without realizing they were being subjected to an outdated concept of Latin pronunciation.

English-speaking botanists have been faced with the same dilemma. However, Stearn (1983) explains the restored Latin pronunciation together with the corrupted English pronunciation.

Restored Latin is the best hope of English-speaking entomologists to be able to communicate names of taxa to entomologists whose native language is something other than English, and to convert international congresses of entomology from something other than towers of Babel. Our objective should be to promote international communication by having a standard system for pronouncing scientific names. It should not be to perpetuate a corrupted, outdated, English mispronunciation of Latin, and even less to foist this on foreigners as being "Latin." Pronunciation of Latin vowels, consonants and diphthongs according to the restored system is explained in Table 18. It should not be difficult to learn, especially by anyone who has studied Italian or Spanish. It is further explained in modern textbooks on Latin grammar and in modern Latin dictionaries.

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Propagative Transmission

Transmission of an arthropod transmitted disease wherein the causal organism does not undergo cyclical changes, but multiplies in the body of the arthropod vector.

▶ Mechanical Transmission
▶ Cyclo-Developmental Transmission
▶ Cyclo-Propagative Transmission

Propagule

A general term used to describe a reproductive (propagative) stage that will give rise to a new organism, usually in plants (seeds, corms, bulbs) but also in invertebrates (eggs, cysts).

Prophylactic Control

Preventative control. Control procedures implemented in a pre-emptive manner to avoid the possibility of damage.

Propleuron

A lateral portion of the prothorax.

▶ Thorax of Hexapods

Propolis

The resins and waxes collected by bees and used in construction of nests, and in sealing cracks in the nest wall.

Proprioreceptor

An internal sensory receptor that senses the internal body condition including relative position of a body's components.

Propupa

The first of the quiescent instars in Thysanoptera; this stage lacks functional mouthparts.

Prosopistomatidae

A family of mayflies (order Ephemeroptera).

▶ Mayflies

Prosternum

The sclerite between the front legs.

▶ Thorax of Hexapods

Prostomidae

A family of beetles (order Coleoptera). They commonly are known as juglar-horned beetles.

▶ Beetles

Prostomium

A preoral, unsegmented portion of the body, anterior to the first true body segment. This is also known as the acron.

Protease

An enzyme that degrades proteins.

Protein

The polymeric compounds made up of amino acids.

Protelean Parasite

A insect that develops parasitically during the larval stage, and kills the host. The larva kills but a single host, and the adult stage is free living. A more popular term for this is "parasitoid."

Proteneuridae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Protentomidae

A family of proturans (order Protura).

► Proturans

Proteomics

The science and process of analyzing and cataloging all the proteins encoded by a genome (a proteome). Currently the majority of all known and predicted proteins have no known cellular function. Determining protein function on a genomewide scale can provide critical clues to the metabolism of cells and organisms. Proteomics involves understanding the biochemistry of proteins, processes and pathways. Two-dimensional gel analyses were used in the late 1970s to identify proteins active (expressed) in different tissues at different times. Now, biological mass spectrometry is a powerful method for protein analysis, involving identification or localization of proteins and interactions of proteins.

Prothoracic Glands

Endocrine glands found in the thorax and secreting molting hormone (ecdysone) or a closely related ecdysteroid. They are activated by PTTH during the immature stage, and degenerate during or soon after metamorphosis.

► Ecdysone Agonists
► Ecdysteroids
► Endocrine Regulation of Insect Reproduction
► Metamorphosis
► Prothoracicotropic Hormone

Prothoracicotropic Hormone

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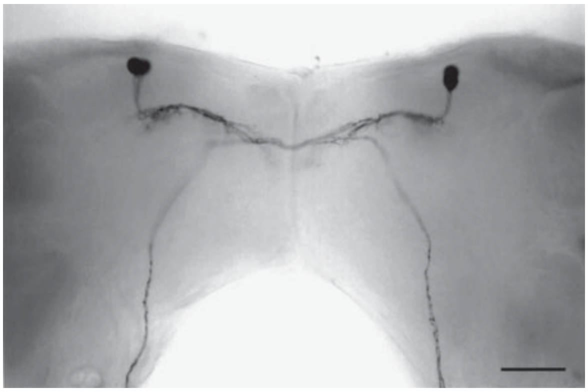
The growth and molting of insects are cyclical phenomena and are brought about predominantly by two hormones, one produced by neurosecretory cells in the insect's brain, and the other by glands in the prothorax, the prothoracic glands. Periodically, specific neurosecretory cells of the brain synthesize a hormone, the prothoracicotropic hormone (PTTH), that acts on the prothoracic glands, which, in turn, respond to this stimulus by synthesizing and releasing a steroid hormone [ecdysone (E), or 3-dehydroecdysone (3-dE), depending upon the species)] that is ultimately converted at target tissues to 20-hydroxyecdysone (20E), the principle molting hormone of insects. 20E then interacts with various target cells via binding to a high affinity nuclear receptor, which then modulates the expression of specific genes and ultimately, regulates cell growth and differentiation. In the case of the epidermal cells, 20E causes them to deposit a new cuticle and, thus, initiates the molting process. The cyclical synthesis and release of PTTH by the neurosecretory cells of the brain is elicited by environmental factors such as photoperiod, temperature, nutritional state, etc. In the case of moths and butterflies, such as the tobacco hornworm *Manduca sexta*, photoperiod and temperature are important and, indeed, the brain appears to possess an extraretinal photoreceptor, i.e., these PTTH-producing neurosecretory cells may be a self-contained unit directly perceiving the light signal, or perhaps the light signal is transduced elsewhere and the information transferred to these neurosecretory cells.

More than eight decades ago, the Polish biologist Stefan Kopeć first suggested that the control of insect molting was mediated by neurohormones. Using larvae of the gypsy moth, he extirpated the brains of these insects and showed that these "de-brained" insects lived for several weeks. If the brains were removed ten days or more after the final larval molt, pupation occurred and brainless, but otherwise normal, moths emerged. However, if the brain was removed prior to the tenth day, the caterpillars failed to pupate (i.e., undergo a metamorphic molt) although they survived for a long time. He also showed that if the larvae were divided into two hemolymph-tight compartments by a ligature posterior to the thorax, both the anterior and the posterior portions pupated simultaneously if tied off after the tenth day, but only the anterior portion pupated if ligation occurred prior to this critical period. Kopeć concluded from these studies that the brain liberates a substance into the hemolymph that is essential for pupation, and that it is released on or about the tenth day after the final larval molt. Indeed, not only was this the beginning of the field of insect neuroendocrinology, but it was also the beginning of the science of neuroendocrinology in general, and led to the now accepted dogma that the nervous system of almost all animals functions as an endocrine gland.

About fifteen years after the work of Kopeć, the great British biologist, Vincent Wigglesworth, showed that decapitation of the blood-sucking hemipteran (bug) nymph *Rhodnius prolixus*, within three or four days after feeding, prevented molting, but that decapitation after this period did not. He concluded that there is a factor within the head (i.e., a portion of the brain) that initiates the molting process. These sorts of experiments have been verified consistently in literally hundreds of species over the past seventy years. Further studies in the 1940s showed that regions of the brain containing large neurosecretory cells were the active portions of this neuroendocrine organ. The classic studies of Piepho (Germany), Fukuda (Japan) and Williams (USA) in the 1940s showed dramatically, again via surgical manipulations, that the brain hormone (PTTH) exerted its effect humorally on the prothoracic glands. When the product of the prothoracic glands was identified as ecdysone in the 1950s, it was hypothesized that PTTH elicited, or enhanced, the synthesis and secretion of ecdysone from the prothoracic glands. This finding of a brain-prothoracic gland (neuropeptide-steroidogenesis) axis was of real interest both to insect physiologists examining the control of insect molting and to those interested in evolution, because this system is quite analogous to the mammalian ACTH-adrenal cortex axis in both a general way, and subsequently, in many details of its transductory biochemistry.

The presence of neurosecretory cells in the nervous system is a very early event in the evolution of animals with data indicating their existence in organisms as primitive as coelenterates (*Hydra*). It should be noted that there are reports that prothoracic glands can also be controlled neurologically by neurons from the brain in some insects, and it has even been suggested that there is direct transport of neurosecretory products by way of channels in the basal lamina, an extracellular matrix that covers all insect tissues. For the most part, however, there is a consensus that PTTH leaves the brain, is stored in a neurohemal organ attached to the brain (the corpus allatum), is released into the hemolymph at specific times and activates the prothoracic gland (Fig. 118).



Prothoracicotropic Hormone, Figure 118 **Immunochemical detection of PTTH in the brain of a day-0 *Manduca sexta* pupa. Note staining in two cell bodies (prothoracicotropes) in each hemisphere of the brain and the crossing of the axon tracts as they move posteriorly to ultimately end in the corpus allatum (not shown) (from Gilbert et al., 2000).**

By the 1970s, investigators began to examine the mechanisms by which PTTH might activate the prothoracic glands to synthesize ecdysone. It was believed by some that in order to study the complex transductory mechanisms involved in ecdysone biosynthesis, it would be much too difficult to work with the whole insect. They therefore attempted, and achieved, a model in which the prothoracic glands of M. *sexta* were placed in a culture medium (in vitro) in which they can live and function in an almost normal way for several weeks. Such glands were shown to synthesize and release 3-dE which was subsequently converted to E and then 20E. It was demonstrated that extracts of the brain of the tobacco hornworm could stimulate the synthesis of 3dE in a consistent and predictable way. Of great importance was the observation that the right and left prothoracic glands of this insect secreted the same quantity of 3dE in vitro so that one gland of a single insect could be experimentally manipulated, with the other serving as the control. With this in vitro assay, a great deal has been learned about how the PTTH signal is transduced into enhanced ecdysteroid synthesis in the prothoracic gland.

The first indication that a mammalian-like signaling mechanism was utilized was the finding that brain extract stimulated the rapid synthesis of cyclic AMP (cAMP) in the prothoracic glands, and that this was followed by 3dE biosynthesis. (In reality, it is the mammal that used an insect-like signaling mechanism because insects evolved several hundred million years before mammals.) With this in vitro bioassay, it was also possible to assay particular parts of the *Manduca* brain as noted previously, and by dissecting out specific neurosecretory cells with an eyebrow hair, it was shown that there were two neurosecretory cells in each side of the brain of the insect that contained PTTH. These so-called prothoracicotropes contained varying amounts of PTTH activity during development. It was shown by immunocytochemical means that axons from these neurosecretory cells extend posteriorly and laterally such that they cross and terminate in the neurohemal organs (corpora allata) where PTTH is stored. Thus, the so-called critical period shown by Kopeć, Wigglesworth and many others is actually the time when PTTH is released from these neurohemal organs into the hemolymph due to one of a variety of environmental and physiological signals. It is of interest that cAMP is also a principal component of the signal transductory cascade in the mammalian ACTH (from the pituitary gland)- adrenal cortex axis.

Most of the data discussed here were generated using PTTH-containing brain extracts to study how PTTH activates ecdysteroid synthesis in the prothoracic glands. Consequently, there have been frequent questions as to whether all the changes in prothoracic gland biochemistry that are elicited by brain extracts are due solely to the effect of PTTH. However, very recently, the *Manduca* PTTH has been cloned, the nucleotide sequence determined and purified, recombinant PTTH produced by transformed cells. The use of this pure, recombinant PTTH in the in vitro system has confirmed all observations on the prothoracic gland that were made using the brain extract.

PTTH-Prothoracic Gland Interactions

PTTH has now been purified and cloned, first from the domestic silkmoth *Bombyx mori*, and subsequently from several other moths (Lepidoptera). The analysis of the PTTH protein and gene sequences indicates that this hormone is synthesized as a prohormone that is processed into a shorter homodimeric molecule (25–30 kDa) as it is transported down the axons of the prothoracicotropes to their termini in the corpus allatum. The structure specified by intra-monomeric, cystine-cystine bonds is essential for the bioactivity of the hormone. Lepidopteran PTTHs clearly comprise a family of proteins, based on the distribution of cystine-cystine bonds, charged amino acids and hydrophilic regions, but these PTTHs are essentially species-specific in action, indicating that the amino acid sequence (primary structure) is likely important for bioactivity. Outside of the Lepidoptera, the structure of PTTH remains conjectural although the PTTH of the fruit fly *Drosophila melanogaster*, appears to be highly glycosylated and considerably larger than those of the moths. These results suggest two possibilities. First, PTTHs have diverged from an ancestral molecule to such a degree that PTTHs from different taxa have only limited structural similarity with minimal amino acid conservation. Second, PTTHs from different taxa (e.g., flies vs. moths) have evolved from different ancestral proteins, and their only similarity is their ability to elicit ecdysteroid synthesis by the prothoracic gland. Current data cannot resolve this issue.

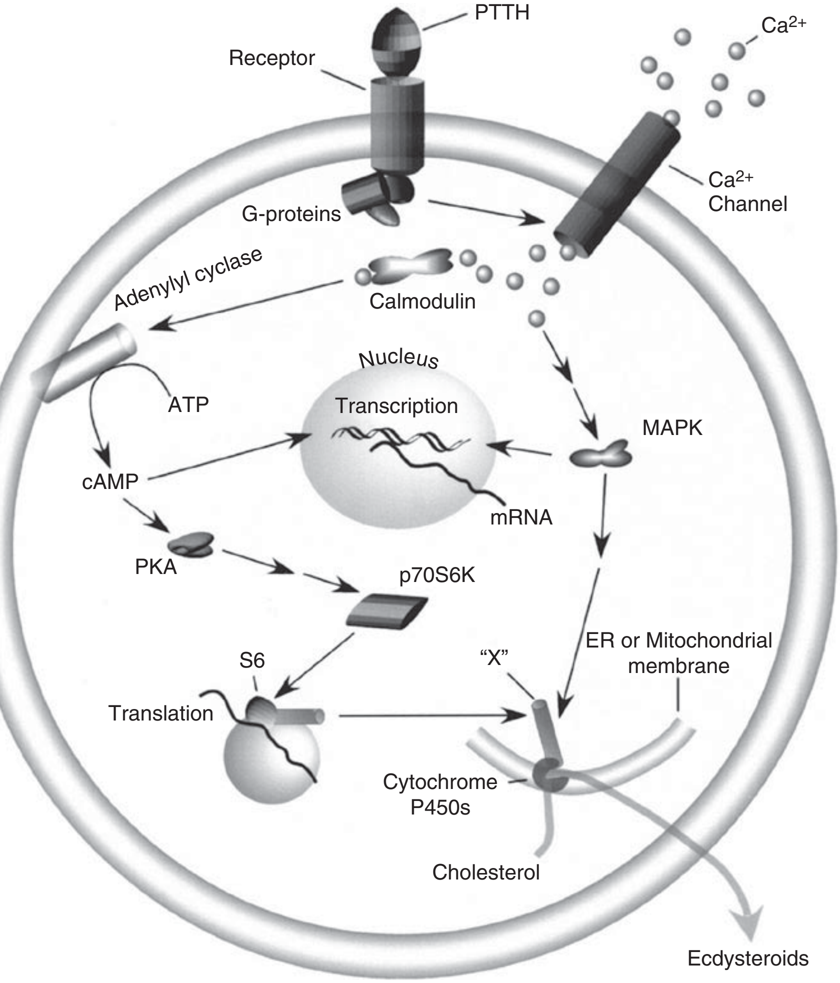
Periodic increases in ecdysteroid titer are critical to pre-adult insect development, as discussed above, and reflect activation of the prothoracic gland by PTTH. PTTH release occurs in particular daily time "windows," following the integration of a variety of factors, such as time since last molt, nutritional status and physical size. How and where such factors are sensed is unknown, but studies do indicate that PTTH release is acutely controlled by the muscarinic class of acetylcholine-releasing neurons. A neuroendocrine modulation of PTTH release has recently been demonstrated in the cockroach *Periplaneta americana*, involving the neurohormone melatonin, which mediates day-night physiological differences in many organisms. While daily cycles of melatonin and PTTH levels are not seen in *Periplaneta*, melatonin could be involved in controlling a daily cycle of PTTH release described in *Rhodnius*.

Changes in PTTH release during *Bombyx* development have been investigated using prothoracic glands in vitro as well as antibodies against PTTH. Although these two approaches were not in complete agreement, both indicate that major peaks of ecdysteroid secretion by the prothoracic gland are preceded by, and partly overlap with, high PTTH titers, and that some episodes of increased PTTH titer are not associated with obvious ecdysteroid production. This latter observation supports the hypothesis that PTTH may have functions in addition to the regulation of prothoracic gland ecdysteroidogenesis.

PTTH may not be the only molecule that stimulates ecdysteroidogenesis by the prothoracic gland, but our knowledge of the nature of other molecules, their biological significance and their modes of action, is rudimentary and preliminary. A brain-derived "small PTTH" (MW < 10,000) of *Manduca* is the best characterized of three candidate factors. Small PTTH stimulates ecdysteroid synthesis in larval glands in vitro, but is only weakly active when applied to pupal glands. Small PTTH appears to stimulate the same second messenger cascades as big PTTH (Ca^{2+} and cAMP: see below), suggesting that it might be an active proteolytic fragment of PTTH, generated during PTTH purification. Conclusive evidence that small PTTH is released into the circulation is lacking. Other candidate ecdysteroidogenic factors that can act upon the prothoracic gland in vitro have been partially purified from lepidopteran proctodaea (*Manduca sexta*, *Lymantria dispar* and *Ostrinia nubilalis*). Given the precedent of the vertebrate gut as an endocrine organ, such findings may not be surprising, but definite roles have yet to be demonstrated in vivo for these incompletely characterized insect molecules. It also would not be surprising if there were negative regulators (inhibitors) of prothoracic gland ecdysteroid synthesis and, indeed, at least two candidate molecules have been isolated, one from fly ovaries and a second from a moth brain, but the in vivo significance of these data remains conjectural (Fig. 119).

The PTTH Transductory Cascade

In the 1970s, studies of the *Manduca* prothoracic gland showed that levels of cAMP, an important intracellular second messenger, were elevated during periods of increased ecdysteroid synthesis (Fig. 119). Further research demonstrated that PTTH stimulated a rapid increase in gland cAMP



Prothoracicotropic Hormone, Figure 119 **A model for the major PTTH-stimulated biochemical events that occur in prothoracic gland cells. Proteins and processes connected by single arrows are likely to be directly interacting, while two arrows indicate the probable interposition of one or more additional proteins or events. PTTH, Prothoracicotropic hormone; cAMP, cyclic adenosine monophosphate; p70S6K, 70 kDa molecular weight S6 kinase; S6, ribosomal protein S6; MAPK, mitogen-associated protein kinase; ER, endoplasmic reticulum; "x," hypothesized, newly synthesized protein that regulates the rate of ecdysteroid synthesis in prothoracic glands stimulated by PTTH.**

content in vitro, detectable within minutes. However, cAMP generation is not the first intracellular change triggered by PTTH. Experiments revealed that cAMP generation was dependent on the influx of extracellular Ca^{2+}, suggesting that cAMP synthesis required Ca^{2+}-calmodulin dependent adenylyl cyclase activity, which is indeed present in prothoracic glands. A variety of Ca^{2+} channels exist in many cell types and it is not clear which type opens in response to PTTH, let alone the mechanism by which PTTH accomplishes this action. G-proteins, small proteins often associated with peptide hormone receptors, may be involved directly in Ca^{2+} channel opening, but other data indicate that cAMP could be involved in such channel regulation. The observation that PTTH stimulates rapid synthesis of cAMP indicates, based on our knowledge of analogous systems in vertebrates, that the PTTH receptor is likely to be situated in the cell membrane, and that binding of PTTH to the receptor is the first step in PTTH signal transduction. Furthermore, the PTTH receptor is predicted to belong to the family of proteins known as G-protein coupled receptors, and to possess an extracellular region that binds PTTH. Nevertheless, knowledge of the earliest events stimulated by PTTH in prothoracic glands is incomplete.

As intracellular levels of cAMP rise, the important cAMP-dependent kinase, protein kinase A (PKA), is rapidly activated in the prothoracic glands. (Kinases regulate the function of other proteins via the addition of phosphate groups.) However, the natural substrates of PTTH-stimulated PKA activity are not known, and a requirement for PKA activity in PTTH-stimulated ecdysteroidogenesis has not been proven unequivocally. It is clear that analogs of cAMP that enter the prothoracic gland stimulate ecdysteroidogenesis and that an inhibitory, stereoisomeric analog of cAMP blocks PTTH-stimulated ecdysteroidogenesis. However, PKA is not the only protein dependent on cAMP for activity, and, therefore, the possibility remains that proteins other than PKA transduce the PTTH signal into eventual ecdysteroid synthesis. For example, a mammalian cAMP-dependent guanine nucleotide exchange factor has been discovered that activates small G-proteins, leading to phosphorylation-dependent events, including the activation of the 70 kDa S6 kinase, a known target in PTTH action.

PTTH stimulates a number of protein phosphorylations in the prothoracic gland via PKA, mitogen-activated protein kinases (MAPKs) and perhaps other kinases. The most prominent and consistent phosphorylated protein is the ribosomal protein S6. The importance of S6 phosphorylation in PTTH-stimulated ecdysteroid synthesis was demonstrated in studies using the drug rapamycin, which blocks S6 phosphorylation by inhibiting the activation of the 70 kDa S6 kinase. In the prothoracic gland, rapamycin inhibits not only S6 phosphorylation, but also PTTH-dependent ecdysteroid and protein synthesis. In vertebrate cells, S6 phosphorylation increases the rate of protein synthesis, especially of mRNAs possessing a polypyrimidine tract at their 5′ transcriptional end, and it is likely that it acts similarly in insect cells. The activation of MAPKs in PTTH-dependent signal transduction has only recently been demonstrated, along with the ability of MAPK inhibitors to inhibit ecdysteroid synthesis. Like the ribosomal protein S6, MAPKs can regulate translation, although by another route, but whether this regulation occurs in the prothoracic glands is currently unknown.

Vertebrate and insect steroidogenic cells share many intracellular mechanisms that function in the regulation of steroid hormone synthesis, as noted previously. In both groups, peptide hormones produced by neurons or brain-associated cells bind to cell membrane receptors associated with G-proteins, with a subsequent generation of cAMP. Increases in intracellular Ca^{2+} occur, as do multiple protein phosphorylations, including that of the ribosomal protein S6. In both taxa, the final transductory step in acutely up-regulating steroid hormone production appears to be the synthesis of one or more short-lived proteins that abolish a rate-limiting bottleneck in the steroid synthesis pathway. In vertebrates, two such proteins are believed to facilitate the movement of cholesterol across the mitochondrial membrane, which is the rate-limiting step in vertebrate steroid hormone production. In insects, the rate-limiting step in ecdysteroid synthesis has not yet been characterized, but recent data from *Drosophila* suggest it may well involve movement of ecdysteroid precursors between intracellular compartments, like the endoplasmic reticulum and the mitochondrion, and that a carrier protein may be involved. Furthermore, it is known that PTTH-stimulated ecdysteroid synthesis in *Manduca* requires protein synthesis, as demonstrated by the ability of translation inhibitors to block PTTH-stimulated ecdysteroid synthesis, and that PTTH stimulates the synthesis of about ten specific proteins.

PTTH might also regulate other cell types besides those of the prothoracic gland. A thorough discussion of this topic is not within the scope of this review, but it is noteworthy that significant levels of PTTH are present in adult brains, by which time the prothoracic glands have disappeared due to programmed cell death. This observation suggests that PTTH likely regulates cellular processes other than prothoracic gland ecdysteroid synthesis.

A number of the important PTTH-related events in the prothoracic gland is now known. However, knowledge about the events that occur in prothoracic gland cells after PTTH stimulation is still fairly incomplete. For instance, nothing is known about possible PTTH-elicited long term changes in the levels of ecdysteroid-synthesizing enzymes (cytochrome P450s) via either translation or transcription, an effect that might be expected based on vertebrate studies. The PTTH-stimulated activation of a mitogen-activated protein kinase is suggestive in this context, as this family of kinases can migrate into the nucleus to regulate transcription. Furthermore, there are enormous gaps in our knowledge of the events that occur between PTTH contacting a prothoracic gland cell and S6 phosphorylation, and between this phosphorylation and the first steps in the conversion of cholesterol to ecdysteroid. It is likely that continued, integrated molecular and biochemical studies of the PTTH control of ecdysteroid synthesis will fill many of these gaps in our knowledge and that major revisions in our current understanding will surely be necessary in the future.

► Ecdysteroids
► Ecdysone Agonists
► Diapause

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Prothoracic Plate

Equivalent to thoracic plate.

Prothorax

The most anterior of the three thoracic segments, bearing the first pair of legs.

► Thorax of Hexapods

Protocerebrum

The largest and most anterior segment of the insect brain, that innervates the compound eyes and ocelli (Fig. 120).

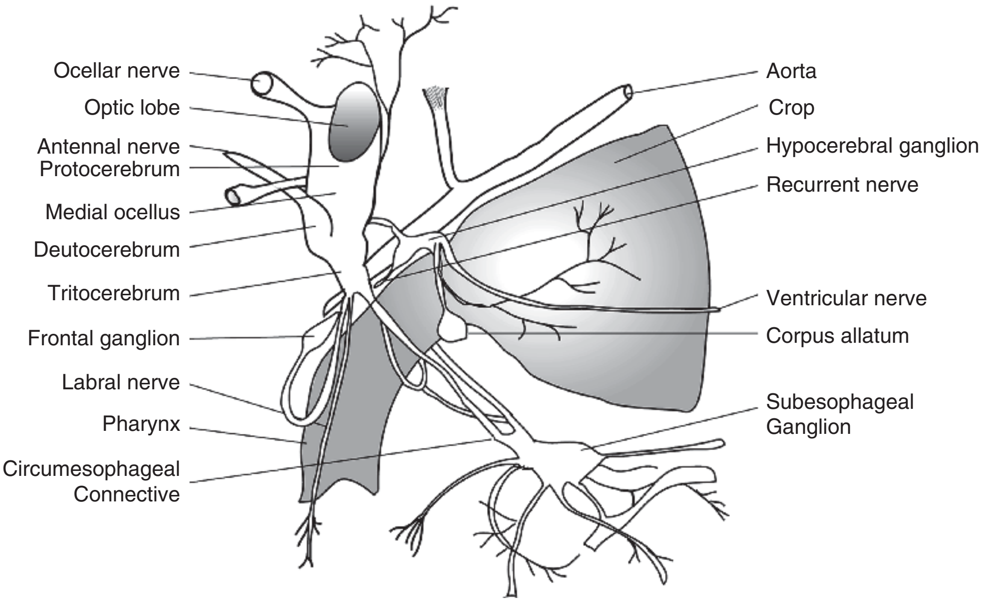
► Nervous System

Protonymph

In mites (Acari), the second instar.

Protopodite

The basal portion of a segmented appendage.



Protocerebrum, Figure 120 **Diagram of the insect brain, lateral view (adapted from Snodgrass, Insect morphology).**

Prototheoridae

A family of moths (order Lepidoptera). They also are known as African primitive ghost moths.

► African Primitive Ghost Moths
► Butterflies and Moths

Protuberance

A projection.

Proturans (Protura)

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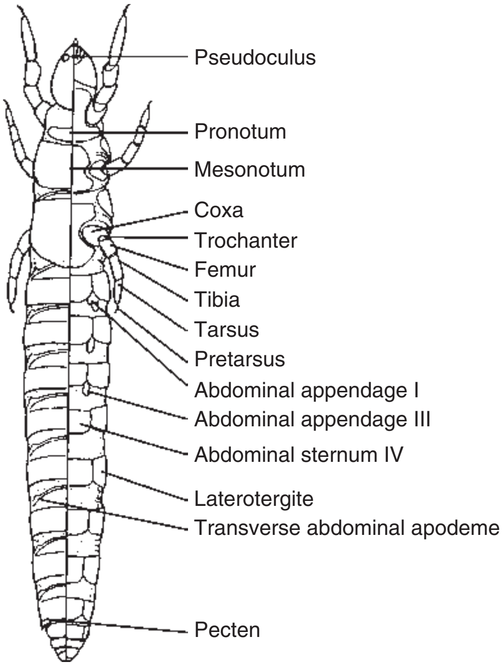
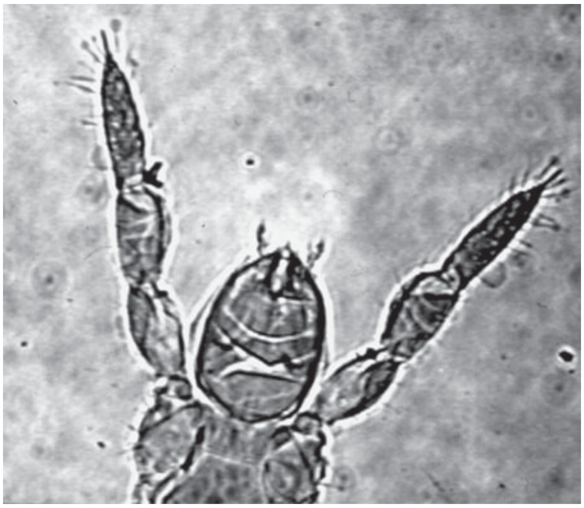
The order Protura consists of minute soil-inhabiting hexapods characterized by the lack of eyes and antenna, a 12 segmented abdomen and development by anamorphosis. The first three abdominal segments have small leg-like appendages that are capable of movement (Fig. 121). The first pair of legs have enlarged foretarsi that are covered with many types of setae and sensilla and function as antenna (Figs. 122 and 123). The first Proturan species discovered, *Acerentomon doderoi*, was described in 1907 by Silvestri. Some researchers believe that Protura is a sister group to the Collembola, though Protura may be a separate class. Here, it is included in the class Entognatha. Protura have a worldwide distribution with over 500 described species divided into two distinct suborders: Eosentomoidea and Acerentomoidea with nine families:

Class: Entognatha
  Order: Protura
    Suborder: Eosentomoidea
      Family: Eosentomidae
      Family: Sinentomidae
    Suborder: Acerentomoidea
      Family: Acerentomidae
      Family: Protentomidae
      Family: Hesperentomidae
      Family: Berberentomidae
      Family: Nipponentomidae
      Family: Acerellida
      Family: Antelientomidae

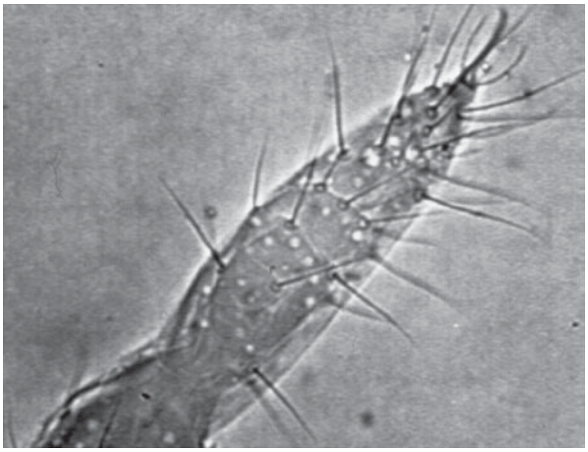
Proturans in the Eosentomoidea possess spiracular openings on the meso- and metathorax



Proturans (Protura), Figure 121 **Diagram of a proturan: left, dorsal view; right, ventral view.**



Proturans (Protura), Figure 122 **Foretarsi of *Eosentomon maryae* Tipping.**



Proturans (Protura), Figure 123 **Close-up of foretarsi showing setae and sensilla.**

connected to a primitive tracheal system. Proturans in the Acerentomoidea are without specialized respiratory structures and respire directly through the cuticle.

Proturans exhibit anamorphosis, a type of development that adds a body segment after a molt. The first stage, or prelarva, is hatched from the egg with nine abdominal segments and weakly developed mouthparts. The second stage or Larva I also has nine abdominal segments but with fully developed mouthparts. Larva II has an additional abdominal segment added between the eighth segment and the telson, or last abdominal segment. The next stage is the maturus junior which has eleven abdominal segments. The maturus junior molts to the adult stage except for males in the family Acerentomidae, which have an additional stage known as the pre-imago. The pre-imago has partially developed internal genitalia. It is not known if the adult stage continues to molt throughout the remainder of its life.

The life-history of Protura is poorly understood. Many species can be found in leaf litter, soil that is rich in organic matter, and dead wood. Similarly, the diet of protura is not well known. Their mouthparts are entognathous and most species appear to have modifications for feeding on fungi; however, some species have styletiform or grinding structures. Like most soil arthropods, proturans most likely feed on a variety materials including plants and fungi as well as scavenging on dead arthropods. In culture, Proturans have been observing feeding on mushroom powder, dead mites, and mycorrhizal fungi.

Protura can be collected from soil and leaf litter with Berlese funnels or by the centrifugation sugar flotation technique. They can be stored in 70% ethanol until mounted on permanent microscope slides with Hoyer's or other clearing medium.

Like many other soil arthropod groups, relatively few proturans have been described by taxonomists. Not surprisingly, distribution records for this group are far from adequate to attempt to understand their biogeography. Undoubtedly, there are many hundreds of species yet to be found from the tropics as well as temperate climate areas.

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Provancher, (L' abbé) Léon

Léon Provancher was born at Bécancour, Quebec, Canada, on March 10, 1820. Educated for the Catholic priesthood and later designated Abbot, he eventually gave up this work due to poor health and moved to Cap Rouge, Quebec. There he devoted his time to the natural sciences, including botany, birds, molluscs, worms, and entomology. In 1869 he began publication of the journal "Le Naturaliste Canadien," which was nearly 8,000 pages long before being terminated for lack of support. Also, he commenced publication of the "Petite Faune Entomologique du Canada," which began with a volume on Coleoptera, published in 1877, and eventually included treatises on Orthoptera, Neuroptera, Hymenoptera, and Hemiptera. He labored on this project until 1890, and his most important contributions are on Hymenoptera and Hemiptera. He described hundreds of insects, including 923 species of Hymenoptera alone. This is a particularly remarkable achievement because he was isolated from libraries and collections. He died at Cap Rouge, Canada, on March 23, 1892.

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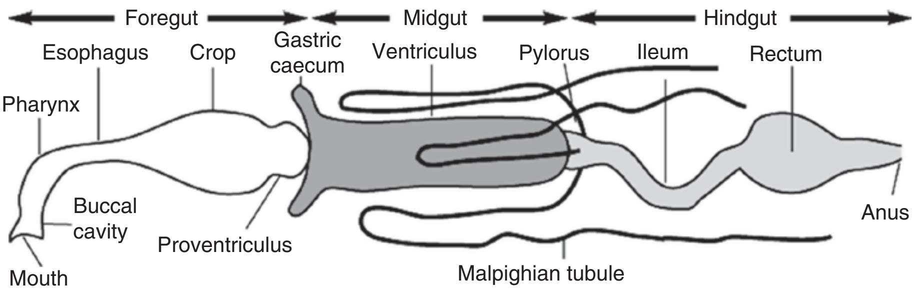
Proventriculus

A valve that controls entry of food into the midgut, and located at the terminus of the foregut (Fig. 124). It is a muscular organ and capable of some grinding action.

► Alimentary System

► Alimentary Canal and Digestion



Proventriculus, Figure 124 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

Proximal

Pertaining to the part of an appendage closer to the body.

Pruinose

Covered with whitish waxy powder. This condition is common in aphids and scales.

Psephenidae

A family of beetles (order Coleoptera). They commonly are known as water-penny beetles.
► Beetles

Pseudergate

In lower termites, a caste from individuals regressing from nymphs, or derived from larvae. In either case, they comprise the worker caste, but can develop into other castes following additional molts.

Pseudironidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Pseudoantagonism

An aggressive response by pollinators to orchids that appear to be invaders of the pollinator's territory. The pollinator's response can result in pollination of the orchids.

Pseudocaeciliidae

A family of psocids (order Psocoptera).
► Bark-Lice, Book-Lice, or Psocids

Pseudococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called mealybugs.
► Scale Insects and Mealybugs
► Bugs

Pseudocopulation

A copulatory response by male pollinators to orchids that mimic females of the pollinator species. The pollinator's response can result in pollination of the orchids.

Pseudo-Curly Top Treehopper, *Micrutalis malleifera* (Fowler) (Hemiptera: Membracidae)

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The pseudo-curly top treehopper or nightshade treehopper, *Micruotalis malleifera* (Fowler), is the only known member of Membracidae to transmit any plant disease agent. This insect was first reported to transmit tomato pseudo-curly top virus (PCTV) in south Florida in 1957. PCTV is now recognized as a member of Geminiviridae based on the inclusion body in the infected cell, serological tests, and sequence evidence. PCTV is transmitted by *M. malleifera* in a semipersistent-circulative manner. Transmission can also be achieved by injecting the treehopper vector with either crude sap or partially purified virus preparation. The transmission efficiency by sap injection is estimated at 30%. Both adults and nymphs are efficient vectors of PCTV. Nymphs retain the virus transmissibility after molting. The transmission efficiency reaches 60% after a 6-h acquisition access period (AAP). The median incubation period of PCTV in *M. malleifera* is estimated at 15 h after a 6-h AAP. The average retention period in the vector is 12 days. Pseudo-curly top disease has been a chronic problem in tomato production in south Florida since the 1940s. The incidence of pseudo-curly top on tomato reaches as high as 50% in some years. PCTV host plants include tomato (*Lycopersicon esculentum* Mill.), eggplant (*Solanum melongena* L.), night shade (*S. nigrum* L.), lettuce (*Lettuca sativa* L.), ragweed (*Ambrosia* sp.), tobacco (*Nicotiana glutinosa* L.), chickweed (*Stallaria medea* L.) and jimson weed (*Datura stramonium* L.).

At 25 ± 1°C using eggplant, nighshade, and ground cherry (*Physalis floridana* Rydb.) as rearing hosts, all *M. malleifera* nymphs display five instars. The average developmental times for instars 1–5 are 4.6, 4.3, 4.4, 5.4 and 7.8 days, respectively, on eggplant; 4.8, 4.5, 4.6, 5.2, 7.6 days, respectively, on nightshade; and 4.6, 4.3, 4.4, 5.4 and 7.8 days, respectively, on ground cherry. The size of instars 1–5 averages as follows: 1.3 mm long and 0.4 mm wide for the first instar, 1.7 mm long and 0.6 mm wide for the second instar, 2.3 mm long and 0.8 mm wide for the third instar, 3.1 mm long and 1.2 mm wide for the fourth instar, and 4.2 mm long and 1.8 mm wide for the fifth instar.

The average adult longevities for females and males are 56.1 and 37.2 days on eggplant, 33.7 and 30.6 days on nightshade and 12.0 and 10.6 days ground cherry, respectively. The adult female is 4.6 mm in length and 2.5 in width. The male is 4.2 mm long and 2.2 mm wide. The eggs are deposited mainly on terminal stems and petioles, but often eggs are found on eggplant leaves. The eggs are imbedded under the epidermal layer with a portion of the egg exposed. The egg is translucent, with one blunt end, and averages 0.9 mm long, 0.3 mm wide. At 25 ± 1°C, the average egg incubation period is 13.6 days (range: 12–16 days). The mean preoviposition period is 3.6 days. The oviposition period is 51.3 days on eggplant. The average number of eggs per day per female is 2.04. The average number eggs laid per female is 55. Both nymphs and adults are very placid and docile.

Tomato pseudo-curly top is not an economically important problem in tomato production areas. Nightshade plant is the main host for both PCTV and *M. malleifera*, which can be effectively controlled in the field and the adjacent areas.

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Pseudomyiasis

Myiasis of the intestinal tract (=enteric myiasis) resulting from accidental ingestion of eggs or larvae of flies. The flies involved usually are members of the families Muscidae and Sarcophagidae, and the myiasis is only temporary.

► Myiasis

Pseudophasmatidae

A family of walkingsticks (order Phasmatodea). They commonly are known as striped walkingsticks.

► Walkingsticks and Leaf Insects

Pseudopod

A soft, foot-like appendage, especially on larvae of Diptera.

Pseudopositor

A tube-like modification of the tip of the abdomen in certain female insects.

► Abdomen of Hexapods

Pseudoparasitism

A response by parasitoids to orchids that are apparent potential hosts. The parasitoid's response results in increased pollination of the orchids.

Pseudostigmatidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Psilidae

A family of flies (order Diptera). They commonly are known as rustflies.

► Flies

Psilopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Psocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Psocids

Members of the insect order Psocoptera.

► Bark-Lice, Book-Lice or Psocids

Psocoptera

An order of insects, formerly known as Corrodentia. They commonly are known as bark-lice, book-lice, or psocids.

► Bark-Lice, Book-Lice or Psocids

Psoquillidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Psychiatry and Insects: Phobias and Delusions of Insect Infestations in Humans

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Insects are an integral and influential part of our culture, as illustrated by their infiltration of our language, arts, history, philosophy, and religion. However, as human society has become progressively more urbanized, insects have become progressively more estranged. As significant but increasingly intangible elements of our culture, insects now feature prominently in certain psychiatric disorders, much as do religious and extraterrestrial elements. Our perception of insects can range from appropriate apprehension when faced with the possibility of a bee sting, through subclinical and clinical insects phobias, to full blown psychotic delusions of insect attacks and infestations. Here we examine firstly phobias about insects, or entomophobia, which includes acarophobia (scabies) and arachnophobia (spiders). Secondly, we deal with the rarer and more serious delusions about insects which are experienced in some psychiatric disorders.

Most people are at least wary, if not fearful, of certain insects (more correctly arthropods). This may be a reasonable fear based on knowledge or experience (bees, wasps, spiders, mosquitoes), an unreasonable but culturally understandable repulsion (cockroaches or flies), or a misplaced fear resulting from inadequate information (dragonflies, moths, crickets). A true insect phobia, on the other hand, is defined as a "persistent irrational fear of and compelling desire to avoid insects," which results in significant distress in the sufferer despite recognition that the fear is excessive or unreasonable. The syndrome represents only the tip on an iceberg, with much unnecessary avoidance behavior never reaching a level where medical attention is sought or necessary.

Although insect phobias probably occurred before recorded history, insects are less likely to have been phobic objects in the past. In hygienically urbanized western societies, many people have little first hand experience of insects other than common flies, mosquitoes, cockroaches and ants. Such urban societies are not as mentally or physically prepared for arthropod encounters as are rural communities.

It is not unreasonable to assume that the danger and annoyance insects have caused to man over the millennia has resulted in an ingrained fear of insects in most societies. Bites and stings to humans and domestic animals act not only as stimulators of toxic and allergic reactions, but insects have been the vectors of potentially fatal diseases since prehistoric times (e.g., dengue or malaria). This explanation, however, is likely to account only for some cases at the non-clinical end of the phobic spectrum, not the genuine phobias which satisfy the definition given above. In the latter clinical cases, as in other phobias, the more likely cause is a displacement of diffuse anxiety to an external focus which can be avoided. The choice of insects as the phobic object may be random, symbolic, or perfectly logical. When symbolic the insects often represent filth and soiling. An example of a "logical" choice of insects as phobic objects is illustrated by the example of a 3-year old girl with an insect phobia, whose symptoms resulted from her being told that her sister with pneumonia had died from a "bug"!

Treatment for entomophobia (and other phobic disorders) is highly specialized, and is largely determined by the therapist's individual preferences. Methods which have been applied in the past include supportive psychotherapy, desensitization, insight psychotherapy, drug therapy (anxiolytics), modeling, hypnotic regression and reframing, implosive therapy, and combinations of these therapies.

Some detailed information about which insects are dangerous and which are not is probably one of the most useful things that an entomologist can contribute to people unfortunate enough to suffer from this disorder. For example, as most entomologists will know, dragonflies are quite harmless, despite their fearsome name and the fact that they feature as phobic objects in many a person's entomophobia. It is useful to remember that only blood feeders (mosquitoes, fleas, ticks, bedbugs) actively pursue humans. The more common phobic objects (spiders, bees) never bite or sting unless trapped or seriously threatened. The former category comprises insects which are associated with poverty or poor sanitation, but perhaps surprisingly, insects in the latter category are feared the most despite being beneficial to man.

"Delusions of parasitosis" can be defined as an unshakeable false belief that live organisms are present in the skin. The disorder was first described in 1894 by Thibierge, who named it acarophobia. Confusingly the syndrome has also been referred to as dermatophobia, parasitophobia, and entomophobia. In 1946 Wilson and Miller more correctly referred to the disorder as delusions of parasitosis. The "offending" organisms range from insects to worms and bacteria, the type often depending upon the parasitological knowledge of the patient. Delusions of parasitosis constitute a symptom complex rather than a disease entity, and are found in a variety of physical and mental diseases. The condition can be difficult to differentiate from entomophobia, particularly when there is a phobia of infestation. Patients with delusions of parasitosis actually experience the state of being infested. This is fundamentally different from having a fear of becoming infested, which falls into the category of entomophobia. Even though the syndrome is a psychiatric disorder, patients usually visit a dermatologist rather than a psychiatrist, since they are convinced they have a dermatological problem. Referral to a psychiatrist is nearly always rejected, and the dermatologist has the difficult task of treating these patients.

The syndrome may be preceded by an original and very real arthropod infestation acting as a "trigger." Other possible triggers include the itch resulting from systemic disease (diabetes, TB, syphilis) or from alcohol withdrawal ("the DT's" – delirium tremens). The sufferer usually complains about itching, biting, stinging, burning and crawling sensations. Insects are often described as black or white, jumping, and sometimes emerging from cosmetics or toothpaste. The "matchbox" sign is ominous, where the patient brings unidentifiable specimens to the doctor or pest controller at the first visit. Microscopic examination of the contents usually reveals only lint, scabs, or other household dust. Such negative findings invariably lead to more intense collection and presentation of specimens by the sufferer. One can often elicit a list of attempted treatments including all imaginable varieties of detergents, balms and poisons. Thus there may be excoriations produced by the fingernails on the skin as well as signs of chemical burns as a result of attempts to kill the parasites. The patient is compelled to dig the parasites out, especially before going to bed, and often resorts to the use of a knife, tweezer or other sharp implement, leaving skin lesions consistent therewith.

Because of the variety of diseases in which delusions of parasitosis occur, there is no generally accepted approach to treatment. Psychotherapy and psychoanalysis have been successful in treating delusions of parasitosis associated with repressed conflicts over sexuality and aggression, and drug treatment can provide significant relief of both itch and delusions. A number of other treatments are used less frequently or have fallen out of favor (including ECT – electroconvulsive therapy).

The prognosis is quite variable, and often dependent on those other diagnosed or undiagnosed diseases which contribute to the symptomatology. The itch (formication) of delirium tremens, for example, has an excellent prognosis, but the prognosis is worse in schizophrenia. The prognosis in patients suffering from paranoid conditions is very poor, because these cases are usually not very subjectable to effective treatment. One author describes paranoiacs who would dig into their skins "up to the time of involuntary parting, and who probably still dig, under somebody else's auspices"!

The details of natural history of the infesting organisms related by patients are often quite complex, and depend upon the patients' previous entomological knowledge. Imagined animals range from fleas, lice and scabies through itchmites, bedbugs and worms, to nondescript "black things" and insects new to science. The therapist must assess the feasibility of these details by consulting medical entomology texts or local entomologists. It is important to remember that psychiatric patients can be the unwilling hosts of real lice, mites, and bedbugs as easily as can anyone else.

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Psychidae

A family of moths (order Lepidoptera). They commonly are known as bagworm moths.

▶ Bagworm Moths
▶ Butterflies and Moths

Psychodidae

A family of flies (order Diptera). They commonly are known as moth flies and sand flies.

▶ Flies

Psychomyiidae

A family of caddisflies (order Trichoptera). They (as well as Polycentropodidae) commonly are known as trumpet-net and tube-making caddisflies.

▶ Caddisflies

Psychopsidae

A family of insects in the order Neuroptera.

▶ Lacewings, Antlions and Mantidflies

Psyllidae

A family of insects in the order Hemiptera. They sometimes are called psyllids or lerp insects.

▶ Bugs

Psyllids

Members of the family Psyllidae (order Hemiptera).

▶ Bugs

Psyllipsocidae

A family of psocids (order Psocoptera).

▶ Bark-Lice, Book-Lice or Psocids

Pteridophagy

Fern feeding. Arthropods that feed on ferns are said to be pteridophagous or pteridophages. Surprisingly few insects feed on ferns; most are associated with the more modern angiosperms. The relative lack of insect feeding on ferns is attributed to both chemical and morphological attributes of ferns, though several groups of insects have adapted to use ferns as a food substrate. Most pteridophagous insects are moths (Lepidoptera), and include members of the families Tineidae, Oecophoridae, Pyralidae, Callidulidae, Geometridae, and Noctuidae, though fern feeding is not limited to moths.

▶ Food Habits of Insects

Pterolonchidae

A family of moths (order Lepidoptera). They are commonly called lance-wing moths.

▶ Lance-Wing Moths
▶ Butterflies and Moths

Pteromalidae

A family of wasps (order Hymenoptera).

▶ Wasps, Ants, Bees and Sawflies

Pteronarcidae

A family of stoneflies (order Plecoptera). They sometimes are called giant stoneflies.

▶ Stoneflies

Pterophoridae

A family of moths (order Lepidoptera). They commonly are known as plume moths.

▶ Plume Moths
▶ Butterflies and Moths

Pterostigma

The dense, often discolored portion of the costal margin of a wing, usually at the end of the radius. This is also known as the stigma.

▶ Wings of Insects

Pterothorax

The fused meso- and meta-thorax found in certain winged insects.

▶ Thorax of Hexapods

Pterothysanidae

A family of moths (order Lepidoptera) also known as Parnassian moths.

▶ Parnassian Moths
▶ Butterflies and Moths

Pterygote

An insect bearing wings, or derived from winged ancestors. A member of the Class Insecta, subclass Pterygota.

Pthiraptera

An order name in some classification systems, and comprised of Mallophaga (chewing lice) and Siphunculata (sucking lice).

▶ Chewing and Sucking Lice

Pthiridae

A family of sucking lice (order Phthiraptera). They sometimes are called pubic lice.

▶ Chewing and Sucking Lice
▶ Human Lice

Ptiliidae

A family of beetles (order Coleoptera). They commonly are known as feather-winged beetles.

▶ Beetles

Ptilinum

An inflatable organ on the front of the head, thrust out from a suture just above the base of the antennae, in higher flies. It is expanded when the adult insect is escaping from the puparium.

Ptilodactylid Beetles

Members of the family Ptilodactylidae (order Coleoptera).

▶ Beetles

Ptilodactylidae

A family of beetles (order Coleoptera). They commonly are known as ptilodactylid beetles.

▶ Beetles

Ptiloneuridae

A family of psocids (order Psocoptera).

▶ Bark-Lice, Book-Lice or Psocids

Ptinidae

A family of beetles (order Coleoptera). They commonly are known as spider beetles.

▶ Beetles

PTTH

Abbreviation for prothoracicotropic hormone.

Ptychopteridae

A family of flies (order Diptera). They commonly are known as phantom crane flies.

► Flies

Pubescence

A covering of setae (hairs).

Pubescent

Covered with hair-like structures (setae in insects, trichomes in plants).

Pubic Lice

Members of the family Pthiridae (order Phthiraptera).

► Chewing and Sucking Lice

►Human Lice

Puddling Behavior by Lepidoptera

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Visitation of mud puddles and patches of moist soil – puddling – is common among many Lepidoptera, as well as other insects such as leafhoppers (Cicadellidae). The phenomenon is most conspicuous among brightly colored butterflies that often form large aggregations at roadside puddles, along streams, or beside pastureland ponds. Among butterflies such as pierids and swallowtails, the presence of one individual often serves as a catalyst for the formation of these aggregations. Puddling is also common among many species of moths and leafhoppers, which are more scattered on the soil at night and do not form the spectacular mud-puddle clubs often seen in diurnal Lepidoptera (Fig. 125).

Puddling Behavior by Lepidoptera, Figure 125 Streamside aggregation of puddling pierid butterflies.

Some puddling species of Lepidoptera pump water through their guts, exuding droplets of water from the tip of the abdomen. Certain species of notodontid moths sit on a film of water and pump large quantities of fluid through their guts, discharging up to 8.5 ml/h in rhythmic jets up to 30 cm. Even dry patches of soil are visited by some species of butterflies and moths that can moisten the substrate with a bead of saliva passed down the proboscis. Some skippers moisten the substrate by flexing the tip of the abdomen beneath the body and exuding a drop of fluid that they reimbibe.

Although puddling behavior can have different functions such as acquisition of water and thermoregulation, it is believed to play an important role in the procurement of salts, particularly sodium, which is in short supply for many herbivorous insects. Sodium can increase reproductive success significantly for both males and females. Whether the insects are butterflies, moths, or leafhoppers, the sex ratio typically is exclusively or predominantly in favor of males. The few females that visit soil are usually old and worn. The explanation for the biased sex ratio lies in the need to acquire salts for mating. When males pass a spermatophore (packet of sperm) to females, they lose a significant amount of salts that can be reacquired most readily from salt-rich sources, particularly soil and animal products such as dung, sweat, urine, and the exudates of carcasses. The dung of carnivores has a greater attraction than that of herbivorous mammals, presumably because of the richer supply of sodium. Females, although they lose a significant amount of sodium when they lay their eggs, are able to replenish their supplies, in part, from sodium in the male's spermatophore, which is passed to the female during mating. In their first mating, males may transfer a third of their abdominal sodium to a female.

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Puffing

A swelling in the giant polytene chromosomes of salivary glands of many dipterans.

Pulicidae

A family of fleas (order Siphonaptera). They sometimes are known as common fleas.

► Fleas

Pulsatile Organ

This is a pulsating heart-like organ. The function is to maintain circulation through the appendages, including the wings.

Pulvillus (pl., pulvilli)

Soft pad-like structures found between the tarsal claws, and the short, stiff hairs on the underside of the tarsal joints.

Punctate

Containing impressed points, punctures, or dimples.

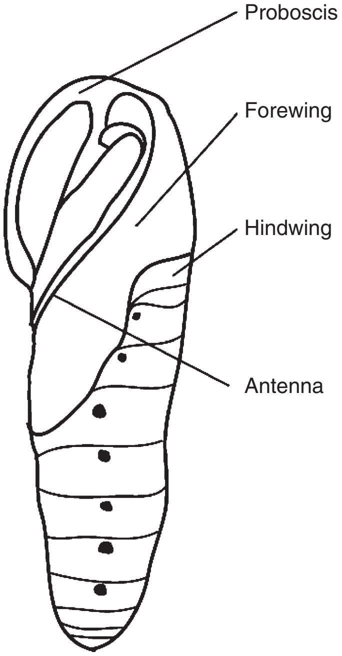
Punkies

Members of the family Ceratopogonidae (order Diptera).

► Flies

Pupa

The nonfeeding, immobile stage between the larval and adult stages in insects with complete metamorphosis. A stage where major reorganization of the body take place (Fig. 126).



Pupa, Figure 126 **Side view of a moth pupa (Lepidoptera: Sphingidae).**

Pupariation

Formation of the puparium by larval Diptera.

Puparium (pl., puparia)

The hardened, thickened integument of the last instar larva of Diptera, in which the pupa is formed.

Pupation

Formation of the pupal stage in holometabolous insects.

Pupiparous

Giving birth to fully developed larvae that are ready to pupate.

Purple Scale, *Cornuaspis beckii* (Newman) (Hemiptera: Diaspididae)

This can be an important citrus pest, but it is susceptible to parasitism.

► Citrus Pests and Their Management

Push-Pull Strategy for Insect Pest Management

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The "push-pull" strategy, a novel tool for integrated pest management programs, uses a combination of behavior-modifying stimuli to manipulate the distribution and abundance of insect pests and/or natural enemies. In this strategy, the pests are repelled or deterred away from the main crop (push) by using stimuli that mask host apparency or are repellent or deterrent. The pests are simultaneously attracted (pull), using highly apparent and attractive stimuli, to other areas such as traps or trap crops where they are concentrated, facilitating their control.

The term "push-pull" was first conceived as a strategy for insect pest management by Pyke, Rice, Sabine and Zaluki in Australia in 1987. They investigated the use of repellent and attractive stimuli, deployed in tandem, to manipulate the distribution of *Heliocoverpa* spp. in cotton to reduce reliance on insecticides, to which the moths were becoming resistant. The concept was later formalized and refined by Miller and Cowles in the US in 1990, who termed the strategy "stimulo-deterrent diversion" while developing alternatives to insecticides for control of the onion fly, *Delia antiqua*.

The development of a reliable, robust, and sustainable push-pull strategy requires a clear scientific understanding of the pest's biology and the behavioral/chemical ecology of the interactions with its hosts, conspecifics, and natural enemies. The specific combination of components differs in each strategy according to the pest to be controlled (its specificity, sensory abilities, and mobility) and the resource targeted for protection.

Among several push-pull strategies under development or used in practice for insect pest control, the most successful example of the push-pull strategy currently being used by farmers was developed in Africa for controlling stemborers on cereal crops. This strategy was developed using technologies appropriate to resource poor farmers and has shown a high adoption rate and spontaneous technology transfer by farmers, resulting in significant impact on food security by increased farm production in the region.

Management of Cereal Stemborers in Africa Through Push-Pull Strategy

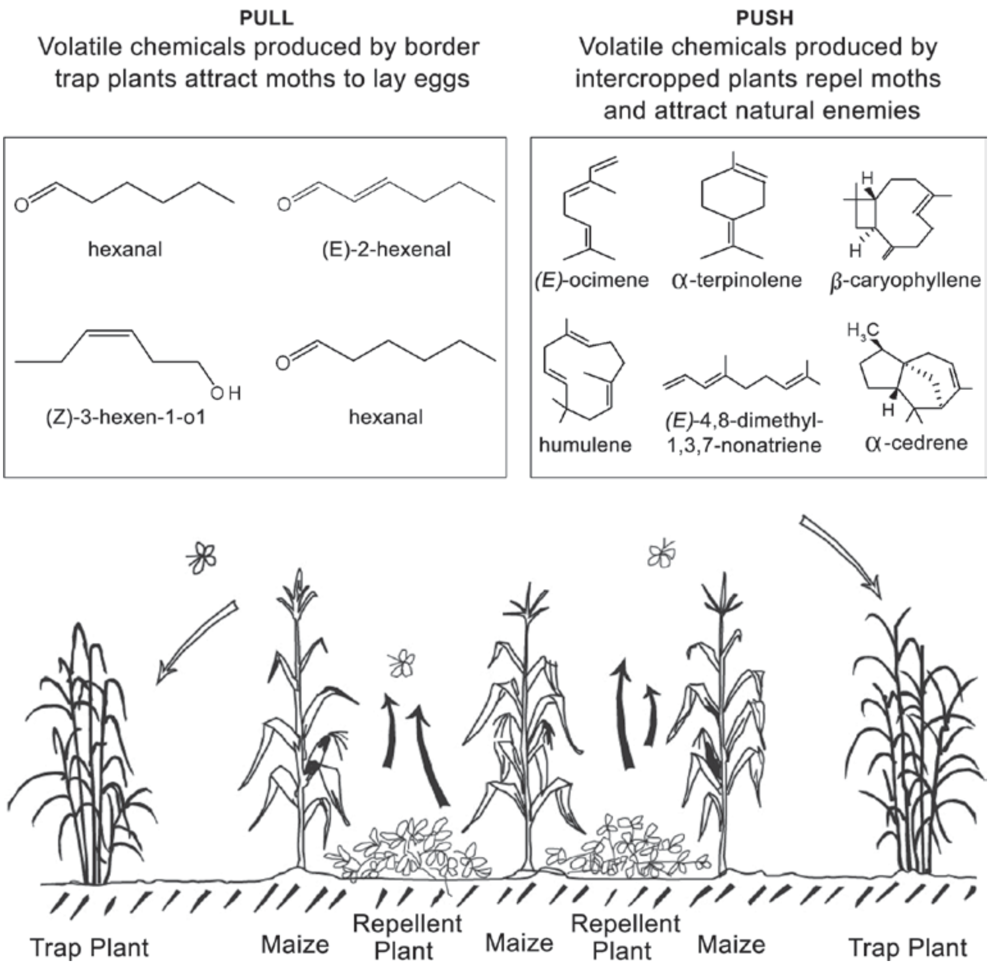
Maize and sorghum are the principal food and cash crops for millions of the poorest people in the predominantly mixed crop-livestock farming systems of eastern Africa. Stemborers are one of the major constraints to increased maize production. At least four species of stem borers (*Chilo partellus*, *Eldana saccharina*, *Busseola fusca* and *Sesamia calamistis*) infest maize and sorghum crops in the region, causing reported yield losses of 30–40% of potential output. Stemborers are difficult to control, largely because of the cryptic and nocturnal habits of the adult moths and the protection provided by the stem of the host crop for immature stages. The main method of stemborer control, which is recommended to farmers by the Ministry of Agriculture in these countries, is use of chemical pesticides. However, chemical control of stemborers is uneconomical and impractical to many resource-poor, small-scale farmers. Therefore, reducing the losses caused by stemborers through improved management strategies is urgently needed which could significantly increase cereal production, and result in better nutrition and purchasing power for many maize and sorghum producers. To put stemborer control within the reach of African farmers, simple and relatively inexpensive measures need to be developed and tailored to the diversity of African farming systems. Several national and international agricultural research centers continue to devote increasingly scarce resources towards the development of technologies intended to increase farm production through stemborer management but with little impact.

A push-pull strategy for managing cereal stemborers in Africa was developed by scientists of the International Centre of Insect Physiology and Ecology (ICIPE) in Kenya and Rothamsted Research in the United Kingdom, in collaboration with other research organizations in eastern Africa. The strategy involves combined use of intercrops and trap crops, using plants that are appropriate to the farmers. This push-pull strategy does not use any chemical deterrents or toxins, but uses repellent plants to deter the pest from the main crop. The trap plants used in this push-pull strategy have the inherent ability of not allowing development of trapped stemborers, thus reducing the number of trapped insects. The strategy also attempts to fully exploit the natural enemies in the cereal farming system.

The push-pull strategy for cereal stemborers involves trapping stemborers on highly attractant trap plants (pull) while driving them away from the main crop using repellent intercrops (push). Plants that have been identified as effective in the push-pull tactics include Napier grass (*Pennisetum purpureum*), Sudan grass (*Sorghum vulgare sudanense*), molasses grass (*Melinis minutiflora*), and desmodium (*Desmodium uncinatum* and *Desmodium intortum*). Napier grass and Sudan grass are used as trap plants, whereas molasses grass and desmodium repel ovipositing stemborers. Molasses grass, when intercropped with maize, not only reduced infestation of the maize by stemborers, but also increased stemborer parasitism by a natural enemy, *Cotesia sesamiae* (Fig. 127). All four plants are of economic importance to farmers in eastern Africa as livestock fodder and have shown great potential in stemborer and striga management in farmer participatory on-farm trials. These innovations have found ready acceptance among the resource-poor farmers in Africa. Although directed at resource-poor farmers, lessons can be learned and applied to organic or low-input agricultural systems. More than ten thousand farmers in eastern Africa are now using push-pull strategies to protect their maize and sorghum from cereal stemborers.

How Push-Pull Strategy Works

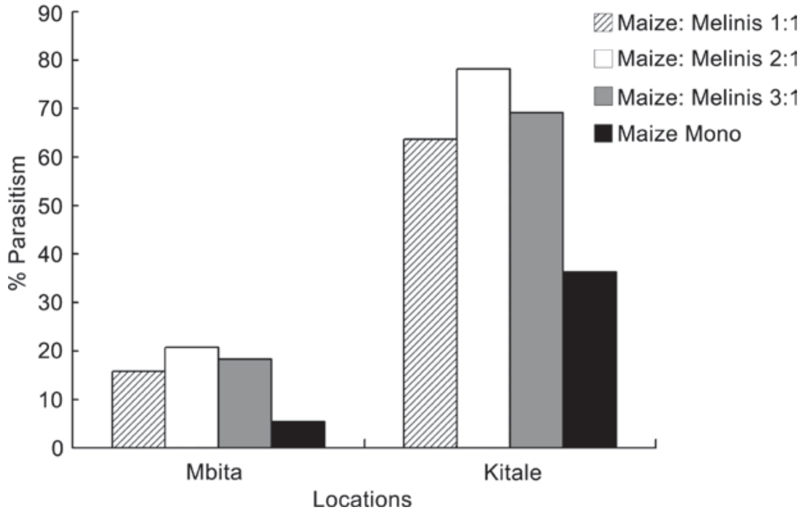
The push-pull strategy undertakes a holistic approach in exploiting chemical ecology and agrobiodiversity. The plant chemistry responsible for stemborer control involves release of attractive volatiles from the trap plants and repellent volatiles from the intercrops. To understand the



Push-Pull Strategy for Insect Pest Management, Figure 127 **A diagrammatic presentation on how push-pull strategy works for cereal stemborers.**

chemical ecology of the push-pull system, volatile chemicals from trap and repellent plants have been investigated using gas chromatography (GC) coupled-electroantennography on the antennae of stemborers and their natural enemies. GC peaks consistently associated with EAG activity were tentatively identified by GC coupled-mass spectrometry (GC-MS), and identity was confirmed using authentic samples.

A general hypothesis developed during this work on insect pests is that non-host plants are recognized by colonizing insects through the release of repellent or masking semiochemicals, although it is almost inevitable that compounds also produced by hosts will be present (Fig. 126). In this case, the host cereal plants and the non-host *M. minutiflora* would be expected to have a number of volatiles in common as they are both members of the Poaceae family. For *M. minutiflora*, five new peaks with EAG activity were identified, in addition to the attractant compounds and others normally produced by members of the Poaceae. These are: (*E*)-β-ocimene, a-terpinolene, β-caryophyllene, humulene, and (*E*)-4,8-dimethyl-1,3,7-nonatriene. Ocimene and nonatriene had already been encountered as semiochemicals produced during damage to plants by herbivorous insects. It is likely that these compounds, being associated with a high level of stemborer colonization and, in some circumstances, acting as foraging



Push-Pull Strategy for Insect Pest Management, Figure 128 **Parasitism of stemborer larvae by *Cotesia sesameae* in maize-*M. minutiflora* intercrops planted in various ratios.**

cues for parasitoids, would be repellent to ovipositing stemborers. This was subsequently demonstrated in behavioral tests. Investigating the legume volatiles, it was shown that *D. uncinatum* also produced the ocimene and nonatriene, together with large amounts of other sesquiterpenes, including α-cedrene.

Six host volatiles were found to be attractive to gravid stemborers: nonanal, napthalene, 4-allylanisole, eugenol and linalool. Recent studies have indicated that the differential preference of moths between maize and sorghum and Napier grass trap crops is related to a large burst of four electrophysiologically active green leaf volatiles released from the trap crop plants within the two hours of the scotophase, the time at which stemborers fly and most oviposition occurs. Although stemborers oviposit heavily on Napier grass, it produces a gummy substance which restricts larval development and only few survive to adulthood.

A trap crop of Sudan grass also increased efficiency of stemborer natural enemies. In a maize field surrounded by a border of Sudan grass, the parasitization of stemborers increased significantly relative to fields without grass borders.

Benefits of Push-Pull Strategy

The principles of the push-pull strategy are to maximize control efficacy, efficiency, sustainability, and outputs, while minimizing negative environmental effects. Although each individual component of the strategy may not be as effective as a broad-spectrum insecticide at reducing pest numbers, the efficacy is increased through tandem deployment of push and pull components. The push and pull components are generally nontoxic and, therefore, the strategies are usually integrated with biological control.

The push-pull strategy developed for stemborers is a good example how basic research can be linked with technology transfer, with farmer participation leading to spontaneous technology transfer between farmers. The push-pull technology has the potential to improve the livelihoods of small-holder farmers and rural families, increase agricultural productivity and improve environmental sustainability. The push-pull strategy, now adopted by more than 10,000 households in 19 districts in Kenya, five districts in Uganda, and two districts in Tanzania has helped participating farmers to increase their maize yields by an average of 20% in areas where only stemborers are present and by more than 50% in areas where both stemborers and striga weed are problems. It constitutes an integrated system that addresses concurrently problems of stemborers, striga weed, soil fertility and soil moisture retention. It opens up significant opportunities for income generation by small-holder farmers and, represents a platform technology around which new income generation and human nutritional components, such as livestock keeping, can be added.

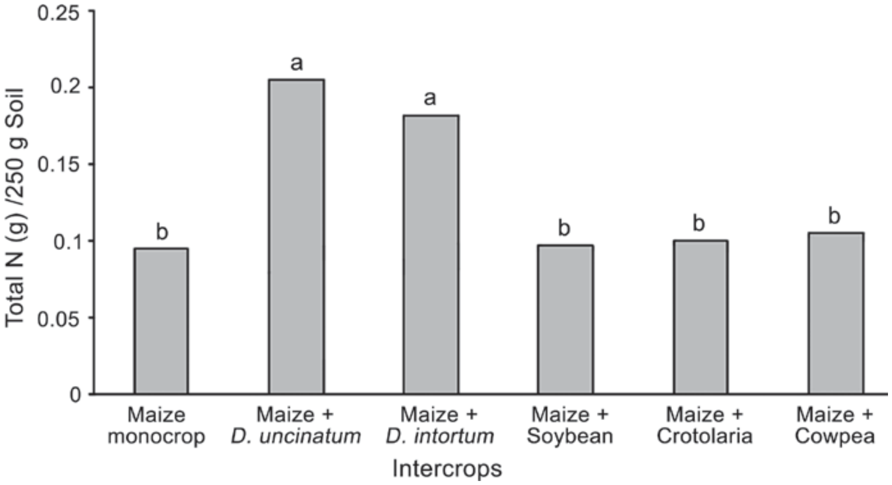
Increased maize yields accompanied by the following additional features of the technology have contributed to the high farmer adoption rates of push-pull technology in eastern Africa:

Reduced Soil Erosion and Increased Soil Fertility

Soil erosion and low fertility are very common problems in eastern Africa. The push-pull strategy has exploited some of the existing practices to address these problems in a multi-functional context. For example, the cultivation of Napier grass for livestock fodder and soil conservation now assumes an additional rationale as a trap plant for stemborer management. Similarly, desmodium, a nitrogen-fixing legume, already grown for improving soil fertility and for quality fodder, is also an effective stemborer repellent and striga weed suppressant. Intercropping desmodium with maize reduces the need for external mineral nitrogen inputs, which are costly and unaffordable by most small-holder rural people, and improves the use efficiency of other inputs. A long-term study in Kenya demonstrated a significant increase in total nitrogen (Fig. 129) on field plots under maize-desmodium intercropping for 3 years than those maize fields intercropped with other legumes.

Striga Weed Control

Witchweed or *Striga* (Scrophulariaceae) are obligate root parasites of cereal crops that inhibit host growth via two processes, competition for nutrients and impairment of photosynthesis. *Striga* infests 40% of Africa's arable land and causes a loss of $7–11 billion to agricultural economy. Among the 23 species of striga prevalent in Africa, *Striga hermonthica* is the most socio-economically important. In western Kenya, it is estimated that 76% of land planted to maize and sorghum, *Sorghum bicolor* (L.) Moench, is infested with *S. hermonthica*, causing up to 100% yield losses equivalent to annual losses estimated at $40.8 million. *Striga hermonthica* infestation continues to extend to new areas in the region as farmers



Push-Pull Strategy for Insect Pest Management, Figure 129 **Total nitrogen (N) levels in the soil under different intercrops in western Kenya (after Khan et al., 2006).**

abandon heavily infested fields for new ones. The push-pull strategy provides significant suppression of striga through intercropping maize or sorghum with desmodium, a repellent plant for stemborers. The protection employed by desmodium in striga suppression has been established to involve a combination of mechanisms ranging from increased availability of nitrogen, soil shading, and an allelopathic root exudation. Exudates from desmodium roots possess striga seed germination stimulation and radical growth inhibition properties which diminish striga seeds through suicidal germination and a continual reduction of the soil seed bank. This combination provides a novel means of *in situ* reduction of striga seed bank in the soil. Additionally, because desmodium is a perennial crop, it is able to exert its striga control effect even when the host crop is out of season, an attribute that makes it a more superior trap crop than most of the other legumes that have been reported to give some limited level of striga control.

Enhanced Biodiversity

Biodiversity in agroecosystems has been reduced greatly in the last decades as a result of intensification of cereal agricultural systems, while empirical data show that agroecosystems with an enhanced overall biodiversity have relatively fewer pest problems. As a result of this observation it has often been stated that enhancement of biodiversity within agroecosystems can greatly contribute to the development of sustainable crop protection systems with a reduced reliance on pesticides. Biodiversity has an intricate role in the functioning of natural and agricultural ecosystems since it performs a variety of ecological services, mediating processes such as genetic introgession, natural control, nutrient cycling and decomposition. Farming practices that conserve such biodiversity as ground fauna and pests' natural enemies may be a practical alternative to manage pests in agricultural systems. Results from Kenya indicate that the push-pull strategy is associated with an overall enhancement of beneficial predator abundance (Fig. 130).

Livestock Production and Human Health

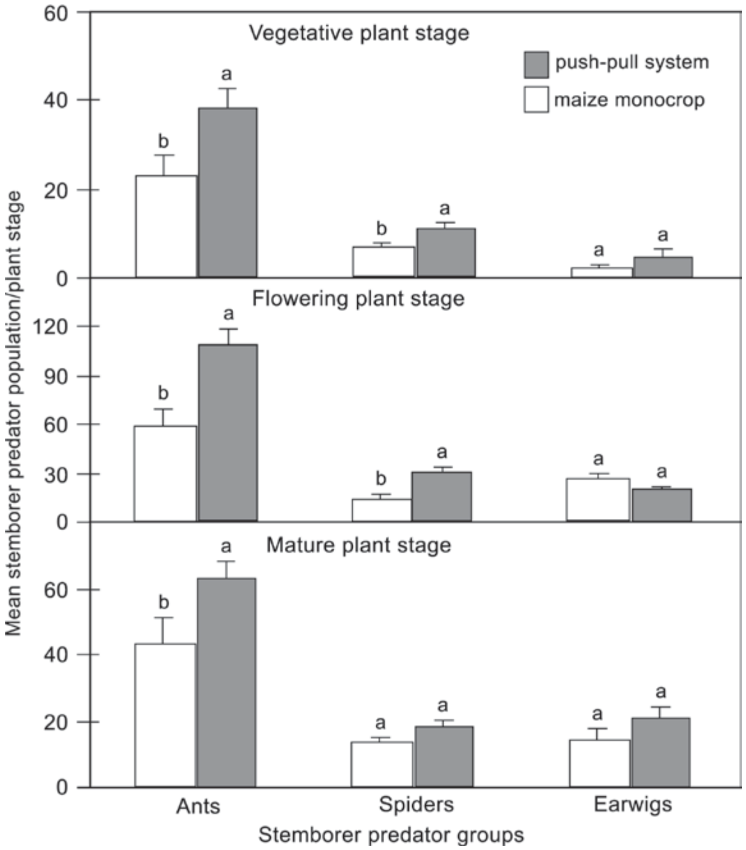
Enhancing the production of fodder plants in local communities demonstrates clear beneficial impacts on health indices, especially for children. By promoting dairy cattle, human health is likely to improve because of high quality milk.

The research outputs have potential to contribute significantly to increased livestock production by providing quality fodder, especially on small farms where pressure for land is high. Dairy cows and dairy goats are emerging as important income alternatives in such situations. With the participation of such partners as Heifer International, more resource-constrained farmers are likely to benefit from dairy animals.

The Suba district of Kenya, a milk-deficit region on the shores of Lake Victoria which has mostly indigenous (zebu) livestock, produced only 7 million liters of milk, far short of the estimated annual demand of 13 million liters. A major constraint to keeping improved dairy cattle for milk production has been the unstable availability and seasonality of feed, which often is low quality. The push-pull strategy, which integrates crop and fodder production, has been adopted by more than 700 farmers in this district. This has resulted in enhanced livestock production and improved milk supply because there now is more and higher-quality feed available for cattle. The number of improved dairy cattle in the district has increased by 500, contributing to a 1 million liter increase in milk production.

Economics of Push-Pull

The contribution of the push-pull strategies to food security cannot be over-emphasized. Intercropping or mixed cropping of maize, grasses and fodder legumes has enabled farmers in Kenya to



Push-Pull Strategy for Insect Pest Management, Figure 130 **Stemborer predator populations at the vegetative, flowering and mature stages of maize plants in Lambwe, Kenya (after Midega and Khan, 2003. Insect Science and its Application 23:301–308).**

increase crop yields, and thus improve their food security and gross benefits. This feature of the technology is suitable for mixed farming conditions, which are prevalent in eastern Africa. Using a semi-structured questionnaire, data were collected on crop performance, stemborer infestation, *Striga* infestation and yield of the different crops. Economic data on input and output amounts, and labor were collected. All crop management decisions were made by the farmers themselves, with technical backstopping from extension staff on management of the desmodium and Napier grass. In addition, baseline information was collected on the households detailing the household sizes and composition, off-farm activities, the farm sizes, the number of cattle, education level of different members of the households and labor availability. An analysis of expenses incurred and revenues accrued in a season was carried out on the push-pull technology and farmers' own practice. The yield of maize from the push-pull technology and the farmers' practice, the revenues generated from all the farm outputs in a season, the expenses incurred to generate that revenue and the gross benefits accruing to the farmers were investigated in the different districts in Kenya. The results showed that although total labor cost and total variable cost were lower in farmers' practice as compared to push-pull fields, total gross revenue and gross benefit of push-pull were significantly higher (Table 19). As important, though less quantifiable, is the reduction in risk that push-pull strategy provides as the build-up of more fertile, water-retaining soil systems give added protection to crops in periods of water shortage and stress.

Future Directions

The push-pull technology for stemborer control is expanding in eastern Africa via small-holder farmers and has significant impacts on food security and income generation for resource-poor maize farmers. On-station and on-farm trials have also demonstrated that push-pull strategies could also be used for control of stemborers in sorghum and millet, and further on-farm research and development is needed to understand the full potential of this strategy for sorghum and millet farmers in arid and semiarid parts of Africa. Pest management options in these regions are affected by low rainfall, the extent to which cattle are kept, and the fact that the cattle are largely free-grazing. However, wherever these approaches are adapted to the specific needs of local farming practices and communities, it is essential that the scientific basis for the modified systems should be clarified and explained by appropriate research.

The major constraint to widespread technology transfer of push-pull has been availability of desmodium seed. Several pathways have emerged, including involvement of a private seed company, community-based seed production, and vegetative propagation among farmers adopting push-pull technologies. The relative merits of these pathways in stimulating autonomous diffusion of the technologies are being analyzed and compared. In addition, the role of different reinforcing interventions such as mass media, information bulletins, field days, farmer teachers, farmer field schools, etc., are being evaluated and the most cost-effective ones will be identified. The relationship between household socio-economic status and land labor ratio in different areas, and the performance of different diffusion mechanisms are also being clarified.

For long-term sustainability of the push-pull system and its placement on a strong scientific foundation, there is also ongoing work on developing tools for quality control of the performance of new push and pull components, to enhance understanding of soil nutrient dynamics in long term push-pull fields, and to study and solve emerging problems of a previously unrecognized pest (a pollen beetle attacking desmodium), and a disease of the companion crops (phytoplasma disease of Napier grass).

Push-Pull Strategy for Insect Pest Management, Table 19 **Economics of push-pull strategy as compared to farmer's practice in six districts in Kenya**

Districts	Total Labor Cost ($)/ha		Total Variable Cost ($)/ha		Total Gross Revenue ($)/ha		Gross Benefit ($)/ ha	
	Push-pull	Farmers' Practice	Push-pull	Farmers' Practice	Push-pull	Farmers' Practice	Push-pull	Farmers' Practice
Trans/ Nzoia[a]	223 ± 1.2	128 ± 1.5	493 ± 1.6	374 ± 2.0	1290 ± 27.7	628 ± 32.4	797 ± 28.0	254 ± 31.0
Suba[a]	167 ± 1.6	134 ± 0.4	278 ± 1.1	250 ± 0.7	679 ± 10.2	329 ± 5.9	401 ± 9.9	79 ± 5.7
Bungoma[b]	247 ± 3.8	222 ± 2.3	331 ± 3.9	300 ± 2.8	867 ± 22.6	415 ± 8.6	536 ± 21.3	115 ± 9.9
Busia[b]	222 ± 1.7	118 ± 0.3	321 ± 1.9	243 ± 0.6	862 ± 11.9	418 ± 2.9	541 ± 12.7	175 ± 2.9
Kisii[b]	184 ± 1.8	140 ± 1.1	246 ± 2.1	210 ± 1.0	733 ± 6.4	334 ± 15.7	487 ± 5.3	134 ± 15.9
Vihiga[c]	227 ± 1.9	128 ± 1.0	359 ± 2.3	331 ± 1.5	785 ± 12	423.1 ± 7.1	426 ± 13.4	92 ± 7.0

Khan et al., unpublished

[a–c] Represent data averages for 7 years, 4 years and 3 years respectively. All the parameters studied were significantly lower in the farmers' practice than in the "push-pull" technology in all the districts ($p < 0.05$)

Current studies in these areas will be continued and tools that emerge will be optimized and incorporated into the push-pull dissemination activities. In addition, several new science-led maize production and protection technologies (such as Bt maize) have been developed by other research institutes, the effectiveness and sustainability of which need to be compared with push-pull strategies over a longer time scale. Questions relating to potential integration of these technologies or their complementarities have been raised and need to be evaluated in continued collaboration with other centers. Demonstration of the relative productivity of integrated approaches and their socio-economics, including the possibility of forward linkages, as well as collaborative undertakings with other institutions, will be important.

From the present example of the push-pull strategy it can be seen that understanding the interactions of plants with insects can yield new ways of exploiting plant defense. Basic science, and particularly understanding the chemical ecology of plant-insect interactions by combined analytical-chemical, neurophysiological and behavioral studies, can lead to practical developments to help resource-poor farmers.

Although the experience to date has been restricted to cereal-based farming systems, we believe that the general approach is applicable to a much wider range of pest problems in a variety of crops, and thus can serve as a model for other researchers in their efforts to minimize pest-induced yield losses in an economically and environmentally sustainable manner. This push-pull strategy for cereal stemborers lays the foundation for still wider application of these principles and serves as a model for the management of other pests in Africa and beyond.

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Putoidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They are sometimes called giant mealybugs.

► Scale Insects and Mealybugs, Bugs

Putzeys, Jules Antoine Adolphe Henri

Jules Putzeys, an early Belgian entomologist, was born at Liège, Belgium, on May 1, 1809. He received a doctoral degree from the University of Liège in 1929, and assumed a successful administrative and judicial career. However, he was fascinated by insects, and studied Lepidoptera, Odonata, and especially Coleoptera. In the case of the latter group, he specialized in Cicindelidae, Carabidae, and Pselaphidae. He served as president of the Entomological Society of Belgium from 1874 to 1876, and remained active in the society afterwards. His most important publications were "Prémices entomolgiques" and "Monographie de *Clivina* et des genres voisins." He died on January 2, 1882.

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Pygidicranidae

A family of earwigs (order Dermaptera).

► Earwigs

Pygidium

The tergum of the last abdominal segment. The supraanal plate. This is the segment often left uncovered by the elytra of beetles.

Pygiopsyllidae

A family of fleas (order Siphonaptera).

► Fleas

Pygmy Backswimmers

Members of the family Pleidae (order Hemiptera).

► Bugs

Pygmy Grasshoppers

A family of grasshoppers (Tetrigidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Pygmy Mole Crickets

A family of grasshoppers (Tridatylidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Pygmy Moths (Lepidoptera: Nepticulidae)

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Pygmy moths, family Nepticulidae, comprise the most minute moths known, with 868 species described in the world from all faunal regions, although most (over 510 sp.) are from the Palearctic region. The total fauna likely exceeds 1,200 species worldwide. The family, together with Opostegidae, forms the superfamily Nepticuloidea, in the section Nepticulina of division Monotrysia, in the infraorder Heteroneura. There are two subfamilies: Pectinivalvinae and Nepticulinae. Adults minute to small (2.5–8 mm wingspan), with head rough-scaled and with a large head tuft of scales, often distinctly colored; haustellum is short and naked (unscaled); labial palpi short, dropping and 3-segmented; maxillary palpi 5-segmented and folded; antennae have an eye-cap developed on the basal segment. Wing maculation is gray or brown, or more brightly colored, sometimes with metallic iridecense. Wing venation is heteroneurous but greatly reduced, with large fringes of hair-like scales on the wing margins and frenular bristles for wing coupling. Adults are diurnally active. Larvae are leafminers, usually blotch mines, although some also mine other plant parts; a variety of host plants are used.

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Pyloric Valve

The valve between the midgut and the hindgut.

Pyralidae

A family of moths (order Lepidoptera). They commonly are known as snout and grass moths.

► Snout Moths
► Butterflies and Moths

Pyrethroids

Synthetic insecticides that are structurally similar to the toxic components of pyrethrum.

► Insecticides

Pyrethrum

Natural insecticide derived from certain plants in the genus *Chrysanthemum*. Pyrethrum is highly valued for its rapid effects on insects and low toxicity to mammals.

► Botanical Insecticides
► Pyrethrum and Persian Insect Powder

Pyrethrum and Persian Insect Powder

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There are numerous examples of plant natural products with interesting agrochemical properties; however, few plant products have had a major role in the development of commercial insecticides. The most important and significant actual application of a plant natural product is pyrethrum or Persian Insect Powder. This powder also has been known as Dalmatian and Japanese powders, or Buhach. The latter powder was produced by the Buhach Producing and Manufacturing Company in California, USA, starting in 1876 from the seeds of Dalmatian pyrethrum.

Pyrethrum powders are made from the dried flowers of several *Chrysanthemum* of the family Compositae. The Persian Insect Powder, obtained from the dried flowers of Persian pyrethrum (*Chrysanthemum coccineum* Willd.), is easily distinguished from those of the Dalmatian pyrethrum (*C. cinerariaefolium* Vis.) by the purple color of the ray florets. As a result, the Persian Insect Powder is darker in color than the Dalmatian Powder. The plants yielding pyrethrum are also known as pyrethrum. Several other species of *Chrysanthemum* such as *C. achilleae* L., *C. myconis* L., *C. parthenium* Bernh., *C. segetum* L., also are recorded to have toxic properties against insects, but *C. coronarium* L., *C. indicum* L., *C. leucanthemum* L. and *C. frutescens.* L. have only negligible toxicity (Fig. 131).

Pyrethrum and Persian Insect Powder, Figure 131 **Pyrethrum powders are made from the dried flowers of several *Chrysanthemum* species, including the Persian pyrethrum (*Chrysanthemum coccineum* Willd.), which belong to the family Compositae. Persian pyrethrum is now principally grown for ornamental purposes and exists in many different horticultural forms and colors.**

History

The use of powdered dry flower of pyrethrum as an insecticide was a long-established folk practice in the Caucasus region and northwest Iran. This powder, known as "Persian Insect Powder" or "Persian Dust," became an article of trade during the eighteenth century and was exported by caravan from Persia, which is now called Iran. It was introduced into Europe in the 1820s, where it was processed and commercialized. The insecticide's efficacy soon became so apparent that the supply reaching Europe was insufficient to meet the demand. The situation changed, however, when an Armenian merchant discovered the secret of its preparation while traveling in the Caucasus and his son started manufacturing the powder on a large scale in 1828. In spite of this, there were still constraints on the supply. Hand collection of the flowers has always demanded low labor costs and, as a result, has limited its major growing regions to developing countries.

The Persian Insect Powder is reported to have been a mixture of the ground flowers of *C. roseum* Adams and *C. carneum* Bieb. Nevertheless, only the former species is distributed in highlands (up to 2,000 m above the sea level) of Armenia, Caucasus and northern Iran and both species may be synonyms for *C. coccineum* Willd. Commercial cultivation of this species started in Armenia in 1828, and continued until 1840, when the greater insecticidal activity of *C. cinerariaefolium* (known as "Dalmatian Pyrethrum" or "Dalmatian Powder") became known.

The Persian Insect Powder was introduced into Europe in 1828 and into the United States in 1876, and then into Japan, Africa, and South America. Parallel to this development, the "Dalmatian Pyrethrum," which exists naturally along the east coast of the Adriatic Sea extending from Italy to northern Albania and up into the mountainous regions of Croatia, Bosnia and Herzegovina, and Montenegro, was cultivated in 1840 in Dalmatia (a historic region along the Adriatic coasts of Yugoslavia, now part of Croatia). The crop was later introduced into many parts of the world. An interesting story traces the discovery of the effect of the Dalmatian pyrethrum to a German woman of Dubrovnik, Dalmatia, who picked a bunch of flowers for their beauty. When they withered she threw them into a corner where, several weeks later, they were found surrounded by dead insects. She associated the death of the insects with insecticidal property of the flowers and embarked in the business of manufacturing pyrethrum powder.

Use and Formulations

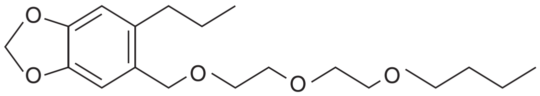
The use of pyrethrum spread rapidly because, in the doses necessary to kill household insects, it is nontoxic to humans and domestic animals. The initial uses of pyrethrum was mainly against insects of public health importance. About 1916, kerosene extracts of pyrethrum flowers appeared on the market and were used widely as sprays against flies and mosquitoes. Until the outbreak of World War II, its principal application was as a dust for household use against bed-bugs, fleas, cockroaches and similar pests. It was not until 1918 that pyrethrum sprays were offered on the market for household use. One of the main uses of pyrethrum today is in the preparation of such sprays. Fly sprays for the protection of cattle were also developed. The main supply now is in the form of extracts in hydrocarbon solvents, concentrated to 25%. Furthermore, mosquito coils made from 1.3% pyrethrum powder are widely used in tropical areas. The slow-burning coils are ignited and the smoke acts both as a killing agent and as a repellent. These coils initially irritate the mosquitoes and then motivate them to fly from the source of the stimuli.

Pyrethrum also is one of the most widely used insecticides for controlling insects in stored products because of its low mammalian toxicity, broad spectrum of activity and short residual life. There are many pyrethrum products formulated for stored products insect control. These range from consumer liquid and aerosol products for control of the insects in private homes, to a wide variety of professional products for use by commercial pesticide applicators. In the latter category, the formulations are either used to protect commodities through direct application to grain (including repellent treatments to packaging material), or for space, contact, and spot treatments within food handling establishments. They include, but are not limited to, bakeries, cafeterias, canneries, commercial airplanes, hospitals, mobile caterers, restaurants, schools and supermarkets.

In agriculture, pyrethrum is unique in being exempt from the establishment of tolerances when applied to growing crops. As a result of having a zero-day preharvest interval, it can be used even on the day of harvest. Furthermore, its broad spectrum of activity as well as its renowned capacity for rapid knock-down allows it to be used against a wide range of agricultural insects. However, because of its very low stability, it is not cost-effective on major crops with large acreages where other insecticides, especially photostable pyrethroids, may be used. Nevertheless, the characteristics listed above make it an ideal insecticide for small fields. In addition, one of the traditional agricultural uses of pyrethrum is a tank-mixture at low application rates (about 10–20 g pyrethrum per ha) with conventional insecticides. This type of mixture exploits the rapid action of pyrethrum on the insect nervous system because insects which are agitated by the action of pyrethrum are exposed to greater quantities of both pyrethrum and the insecticide in the mixture.

Synergists

It has been known since the 1930s that both the knock-down and the killing effects of pyrethrum and some pyrethroids can be greatly optimized by adding synergists that have little or no toxicity alone. During this period, a number of synergists such as sesamin were discovered. Piperonyl butoxide, the most widely used synergist, was the first highly effective synergist found to potentiate the pyrethrum by 5- to 20-fold. Although the mode of action of synergists is not completely understood, one of their activities is believed to inhibit the oxidative and/or hydrolytic metabolism of the insecticide within the insect (Fig. 132).



Piperonyl butoxide

Pyrethrum and Persian Insect Powder, Figure 132 Piperonyl butoxide, the most widely used synergist, is the first highly effective synergist found to potentiate pyrethrum at the range of 5- to 20-fold.

The Pyrethrum Plant

There is considerable confusion in the literature about the taxonomy of pyrethrum (i.e., the plant species from which pyrethrum has been obtained). Recent revisions have even changed the genus *Chrysanthemum* to *Tanacetum*. As a result, the two species of plants with historical and commercial importance, namely the Persian Insect Flower (painted daisy, having red flowers) and the Dalmatian Insect Flower (having white flowers) are respectively considered *Tanacetum coccineum* (Willd.) Grierson and *Tanacetum cinerariifolium* (Trevir) Schultz-Bip, though entomologists continue to refer to these plants as *Chrysanthemum* spp. Both are daisy-like herbaceous perennials belonging to the sunflower family (Compositae).

Pyrethrum is a perennial herbaceous plant which, to the casual observer, resembles the ordinary field daisy. When the plant flowers, many shoots originate from the crown and grow on average to 75 cm. The leaves are petioled and finely cut. The shoots branch a few times before terminating into a white (or red, according to the species), daisy-like flower that consists of a few to several hundred flowers per plant. The flower head of pyrethrum, like any other species belonging to the family Compositae, is a compound inflorescence with small flowers, the florets, aggregated together on a convex receptacle (known as the capitulum). The florets are of two kinds: the disc florets and the ray florets. While disc florets with yellow corollas occupy the center of the receptacle, the ray florets with white corollas form the outer rim of the flower head. The disc florets possess both male and female organs, but the ray florets are unisexual (female alone). In contrast to *C. cinerariaefolium* which possesses white ray florets, the ray florets of *C. coccineum* maybe pink, rose, carmine, crimson or, rarely, white. Moreover, the dried flowers of the latter species is easily distinguished from the former by the purple color of the ray florets and the ten-ribbed achenes (instead of five ribs in *C. cinerariaefolium*). *C. coccineum* produces fewer flowering shoots than *C. cinerariaefolium* and is said to be somewhat more resistant to disease and injury. Commercial flowers vary from 6 to 24 mm in width and from 70 to 300 mg in weight.

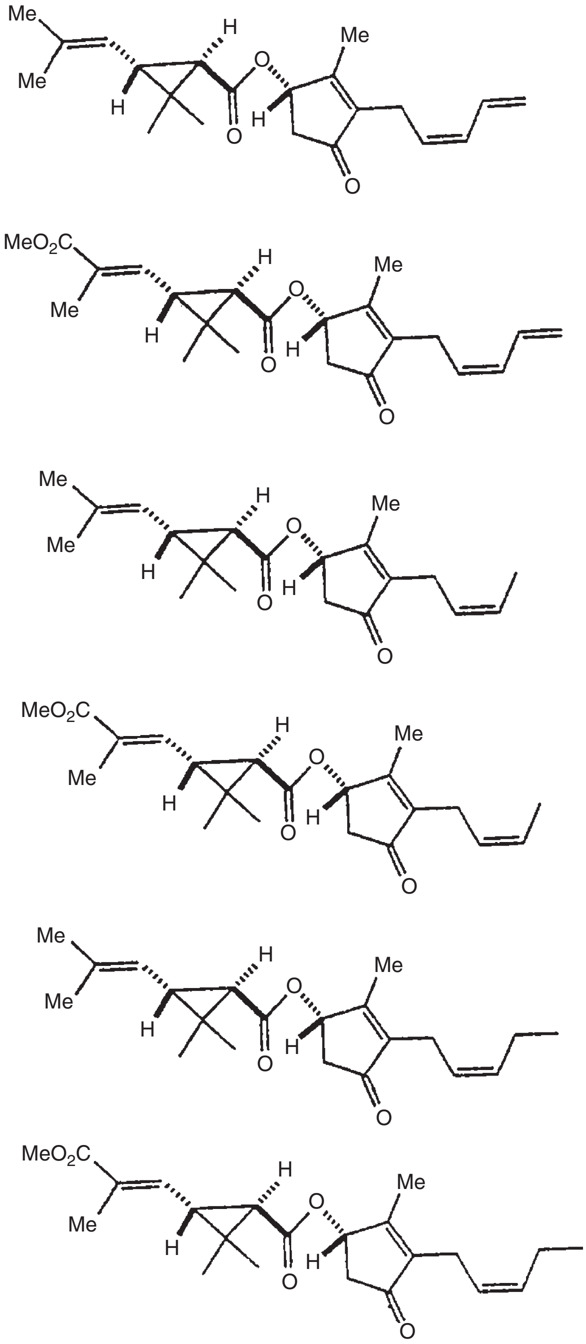
Pyrethrum Production

Pyrethrum propagates easily through different methods including seeds, vegetative splits, stem cuttings rooted under mist and tissue culture. World production of pyrethrum is about 20,000 tons/year. Although the original homes of the commercial flowers of pyrethrum have been Iran, Armenia and Caucasus, a closely related species is now grown in the highlands of East Africa (in particular Kenya, Tanzania, Rwanda and Zaire), Australia (mainly Tasmania), and Papua New Guinea. Eastern Africa, however, remains the main source of supply. For example, from a worldwide production of about 18,000 metric tons in 1992, Kenya alone contributed about 70%. Historically, the major pyrethrum producing countries have been Yugoslavia (until World War I) and Japan (until World War II). By 1941, however, Kenya overtook Japan as the main world producer and Japan ceased to be a significant pyrethrum producer.

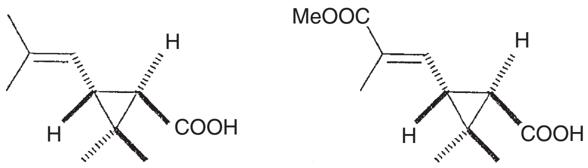
Today, the main commercial source of pyrethrum is the mature flower of *Chrysanthemum* (*Tanacetum*) *cinerariaefolium* Vis., cultivated principally in Kenya and Tanzania at elevations over 1,500 m above sea level. In Kenya, pyrethrum is cultivated almost entirely by about 60,000 small-scale farmers. The crop is not only the main source of cash income for these farmers, but it also provides a major source of export revenue for the country. Pyrethrum cultivation is optimal in the temperatures that occur in the highlands of Kenya (1,800–2,900 m above sea level). Well-drained soils with moderate organic matter are ideal for crop production. New stands in Kenya are established either from seed or from clonal propagation. In commercial plantations of pyrethrum in Kenya, the first picking of mature flowers occurs shortly after flowering and within 3–4 months after transplanting. It is carried out at intervals of 10–14 days and continues for ten consecutive months. At the end of this period, the stand is cut back to remove the dead and unproductive plant material. This practice allows the plant to rest and to get ready for growth in the next season. Flower picking is done by hand, then the flowers are dried and delivered to the factory where crude (oleoresin) as well as high-quality refined extract concentrates are produced. About fifteen parts of pyrethrum flowers are required to produce one part of oleoresin, and up to fourteen parts of oleoresin are required to obtain one part of toxic principle of pyrethrum. A small quantity of fine pyrethrum powder is also prepared for sale to manufacturers of insecticide dusts and mosquito coils. It is interesting to note that *C. coccineum* (the origin of Persian Insect Powder) is now principally grown for ornamental purposes and exists in many different horticultural forms.

Active Ingredients

The actual investigation on the active components of pyrethrum was carried out by two Swiss chemists (H. Staudinger and L. Ruzicka) at Zurich from 1910 to 1916, but their results were not published until 1924. They discovered that the chief insecticidal components of natural pyrethrum consist of six closely related esters (namely, pyrethrin I, pyrethrin II, cinerin I, cinerin II, jasmolin I, and jasmolin II) (Fig. 133). While esters of series I are derivatives of chrysanthemic acid and have excellent insect killing activity, esters of series II which are derived from pyrethric acid have high knock-down



Pyrethrum and Persian Insect Powder, Figure 133 Structures of chief insecticidal components of natural pyrethrum discovered by Swiss chemists at Zurich (H. Staudinger and L. Ruzicka) during the years 1910–1916: From top to bottom: Pyrethrin I, Pyrethrin II, Cinerin I, Cinerin II, Jasmolin I and Jasmolin II.

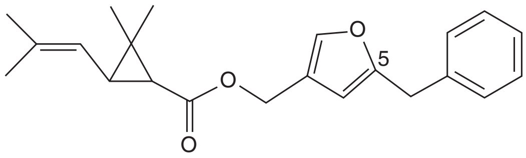


Pyrethrum and Persian Insect Powder, Figure 134 **Structures of chrysanthemic acid (left) and pyrethric acid (right).**

properties. In commerce, flower heads containing at least 0.7% active constituents are extracted by solvents. The extract is then further processed to get a standard 25% concentrate which consists of about 10% pyrethrin I, 9% pyrethrin II, 2% cinerin I, 3% cinerin II, 1% jasmolin I and 1.1% jasmolin II. The amount of insecticidal constituents of pyrethrum varies, depending on the source. While Kenya flowers are the richest, containing about 1.3% active compounds, some strains developed recently may yield over 2% active compounds. It is interesting to note that pyrethrum continues to compete with synthetic insecticides in the specialized areas where selectivity and low environmental hazard are most important. Furthermore, because of the selective and relatively small-scale uses of pyrethrum during the past centuries, there has been relatively little development of insect resistance. In spite of this, the synthetic pyrethroids may threaten the commercial use of pyrethrum in the future because over-application may lead to a proliferation of pyrethroid-pyrethrum cross-resistant insects.

Pyrethroids

Among the classes of insecticides, the aforementioned six molecules (described under active ingredients) are unique for the intensity of their very rapid action against many species of insects and for their minimal hazard to mammals under normal conditions. Nevertheless, all six esters decompose rapidly and lose their insecticidal activity on exposure to air and light. Therefore, the natural compounds and earlier synthetic analogs are generally suitable only for indoor or protected applications.



Pyrethroids, Figure 135 ***Resmethrin*: The first commercially competitive pyrethrin analog developed by the Rothamsted group.**

In fact, the development of the first commercially competitive pyrethrin analog (resmethrin) by the Rothamsted group, led by Michael Elliott, represents an important milestone in agrochemical research (Fig. 135). This discovery subsequently inspired chemical companies to develop a wide spectrum of new synthetic pyrethroids. The discovery of related synthetic pyrethroids stable enough for agricultural applications beginning in the 1970s, has been a revolutionary step toward the production of numerous potent and stable analogs with very low mammalian toxicity. While some pyrethroids are applied with a field rate as low as 2.5 g ha^{-1} (e.g., Deltamethrin), the LD_{50} (acute oral toxicity to rats) of some of them may amount to over 4,200 mg kg^{-1} (e.g., Etofenprox). These analogs, which possess favorable properties like those of the natural compounds and at the same time have much greater potency and stability, now constitute about one-quarter of all the insecticides used worldwide. Surprisingly, the small change in structure between the natural and synthetic products has led to a 34-fold increase in its toxicity to houseflies. The addition of synergists in formulations may still lead to much higher activity.

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Pyrgotid Flies

Members of the family Pyrgotidae (order Diptera).

► Flies

Pyrgotidae

A family of flies (order Diptera). They commonly are known as pyrgotid flies.

► Flies

Pyrochroidae

A family of beetles (order Coleoptera). They commonly are known as fire-colored beetles.

► Beetles

Pyrophilous Insects

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Pyrophilous ("fire-loving") organisms are those that are substantially favored by fire. Pyrophilous species are known among plants, fungi, and animals, including numerous pyrophilous insects. Pyrophilous insects are known from at least 25 families in the orders Hemiptera, Lepidoptera, Diptera, and Coleoptera. As concern about the preservation of biodiversity grows, there is an increasing interest in the effects, positive or negative, of ecological disturbances such as fire on biodiversity. This interest has been reflected by increasing research on the behavior of pyrophilous insects, and on the effects of fire on insect diversity in general.

Sensory Receptors and Behavior

Many species of insects gravitate to newly burned forests because they can use the resources that are available in the recently killed or weakened trees. Some of these insects can evidently detect burned habitats over long distances. Three species, all beetles, have been found that have evolved impressive sensory organs that allow them to locate burned habitats, and also probably help them avoid being burned. Two of these, *Melanophila acuminata* and *Merimna atrata*, are in the jewel beetle family, Buprestidae. The third is an acanthocnemid, *Acanthocnemus nigricans*. The most well-known of these species is *M. acuminata*, which, like most buprestids, is a wood boring beetle in the larval stages. The behavior and physiological adaptations that this beetle displays suggests that it is, to a great extent, dependent on fire for persistence. *Melanophila acuminata* is found throughout the holarctic region and also in parts of the nearctic region. *Merimna atrata* and *A. nigricans* are both found in Australia. The former species is endemic, whereas the latter species has been introduced into parts of Europe, Asia, and Africa.

Melanophila acuminata, *M. atrata*, and *A. nigricans* all contain specialized sensilla that are capable of detecting infrared radiation (IR); however, the morphology and physiology of the IR organs from the three species are very distinct. The IR receptors of *M. atrata* and *A. nigricans* function as very sensitive thermoreceptors that can detect low-level thermal radiation, particularly in the IR range. *Merimna atrata* has four IR receptors, two each on the second and third abdominal sternites. Each is innervated by one multipolar neuron which has a highly branched terminal dendritic mass with a large number of mitochondria. These receptors are similar in structure to the heat-sensitive labial pits found on the lips of boas and pythons. *Acanthocnemus nigricans* has a pair of IR receptors on the prothorax, but these are more complex than those of *M. atrata*. Each receptor is well-supplied with mitochondria, as in *M. atrata*. However, in *A. nigricans*, each receptor has about 30 multipolar neurons. The number and arrangement of the neurons in *A. nigricans* suggest that a mosaic of different temperatures can be detected across the receptor, such as would occur when the beetle is moving laterally or vertically in relation to the IR source. Also, unlike the IR organs of *M. atrata*, those of *A. nigricans* have an air-filled chamber under the cuticle. It has been suggested that this chamber increases the sensitivity of the IR receptors of *A. nigricans*. The IR receptors of *A. nigricans* share striking similarities with those of the pit vipers, a case of convergent evolution in two widely separate taxonomic groups.

Most of the research on IR sensilla has focused on *M. acuminata*. This species usually breeds in dead or dying coniferous trees. These beetles help begin the post-fire decomposition process by ovipositing in newly killed trees. Often this process begins even while the forest is still burning. *Melanophila acuminata* has two metathoracic pit organs. The pit organs are located adjacent to the mesothoracic coxae beneath the legs on each side of the thorax. These pit organs are exposed during flight, but concealed by the legs when not in flight. The pit organs contain 50–100 sensilla. Each sensillum consists of a spherule which lacks an exocuticle but contains a single dendrite. The spherule of each sensillum contains three regions: (i) an amorphous core, (ii) a region of unstructured cuticle with irregular lacunae, and (iii) an outer mantle of helical arranged cuticle. Each spherule is innervated by a single, bipolar neuron which consists of a 25–35 nm ciliary dendrite. The spherule transduces IR radiation into a micromechanical stimulus, which is measured by a mechanoreceptor. Thus, unlike the IR sensilla of *M. atrata* and *A. nigricans*, those of *M. acuminata* act as mechanoreceptors rather than thermoreceptors. Each sensillum in *M. acuminata* is also associated with a wax gland. The wax gland protects the sensillum from dirt, smoke, and desiccation.

Due to the discovery of the metathoracic pit organs in some, but not all, *Melanophila* species, the genus *Melanophila* was reclassified in 1937 and a subgenus *Melanophila* was created to include only the species that have the thoracic pit organs. Two other subgenera (*Phaenops* and *Xenomelanophila*) were created which contained the species that did not have the thoracic pit organs. Seven out of fifteen species in the genus are contained in the subgenus *Melanophila*. All seven of these species possess the thoracic pit organs which function in IR detection. Species that lack the thoracic pit organs do not tend to fly to forest fires. This suggests that the thoracic pit organs are associated with pyrophilous behavior. There are numerous reports of *Melanophila* congregating at fire sources. According to Canadian entomologist William G. Evans, "it is a common observation that species of *Melanophila* often inhabit a dead tree to the exclusion of other borers of freshly killed wood, indicating that they had completely occupied the tree before the other forms arrived."

Evans performed a variety of experiments on *M. acuminata*. He discovered that the pit organs were capable of detecting infrared radiation, which was the first description of an IR-detecting organ in an insect. He found that the beetles responded to infrared radiation by twitching their antennae on the stimulated side. Evans suggested that the IR organs would function tropotactically for long-range orientation, and that thermoreceptors in the antennae would function for short-range orientation.

However, physiological studies contradicted Evans' hypothesis. These studies showed that the antennae of *M. acuminata* reacted to volatiles generated by smoldering wood. They also showed that the beetles are attracted to the forest fires by a combination of olfactory cues and IR radiation. These studies also provided clues on the antennae of female *M. acuminata*. The female's antennae possess 20–30 companiform-like organs, but the function is still unclear. The males' antennae lack these 20–30 companiform-like organs. It was suggested that the organs may assist females in the identification of the optimal or threshold temperatures within the bark for ovipositing of eggs.

There are three factors involved in the ability of *M. acuminata* to detect forest fires using IR receptors: (i) the IR receptors respond to wavelengths between 2.4 and 4.0 nm, with a maximum sensitivity at 3.0 nm, (ii) forest fires burn at temperatures between 435 and 1150°C, which corresponds to the IR wavelengths that *M. acuminata* receptors respond to, and (iii) the atmosphere does not absorb infrared radiation evenly, with very little absorption between 3 and 5 nm. Because these three factors are maximized around 3 nm, IR provides an ideal means for the detection of forest fires.

There is anecdotal evidence that *Melanophila* can detect fires from great distances. A large swarm of *Melanophila* was observed at an oil fire in Coalinga, California. The oil fire reportedly was over 50 miles away from the nearest coniferous forest which would have provided a source of the beetles. The distance that *Melanophila* can detect infrared radiation is estimated to be around 1 km on flat terrain and 5 km for mountainous terrain. The mechanism by which *Melanophila* can detect forest fires from greater distances is unknown, but reports suggest that *Melanophila* beetles are attracted over long distances by smoke from a variety of burning materials including wood, oil, mill refuse, smelter products, and possibly tobacco. Over shorter distances, the beetles are aroused by heat. When a beetle is in the vicinity of the heated source, it will fly quickly and run about over hot surfaces. Reports also suggest that light plays a role in the beetle's attraction to forest fires.

Despite the evidence linking pyrophilous insects with fires, there is still some question regarding the extent to which pyrophilous insects depend on forest fires *per se*. Some have suggested that healthy trees are resistant to attack by *Melanophila*, and that these beetles depend on dying trees for the larvae to develop to maturity. Since fire is not the only mechanism that injures trees to the point of death, it may be that other tree stressors could provide suitable habitat for *Melanophila*. Perhaps fire just provides a convenient means of locating stressed trees.

In addition to specialized sensory organs, some pyrophilous insects have other traits that would seem to be adaptive for an organism that must locate fires over long distances. *Melanophila acuminata* has been found to have lower wing load and greater flight-muscle mass than do closely related non-pyrophilous species, which would seem to be advantageous to an insect that must colonize patchy and unpredictable habitats quickly. These adaptive advantages are underscored by studies showing that *M. acuminata* has lower fecundity than closely related non-pyrophilous species, probably due to the greater size of the pterothorax, which extends deeper into the abdomen in *M. acuminata*, reducing the amount of space for the gonads. *Melanophila acuminata* also have less synchronized development, and emerge over a greater time span, than do closely related non-pyrophilous species. It has been suggested that this is an evolutionary "bet-hedging" strategy to optimize the chances of finding fires that are temporally unpredictable.

Ecology and Natural History

The pyrophilous biota of regions with frequent fires (South Africa, Australia, Mediterranean Europe, and the southern USA) is dominated by vascular plants. In boreal forests, on the other hand, pyrophilous fungi and insects are more common. A possible ecological explanation for this pattern may lie in the greater amount of nutrients in the humus layer of boreal forests. Fire helps to release these nutrients. Since most pyrophilous fungi and insects are decomposers, they may benefit from the increased availability of nutrients after a fire. Many pyrophilous insects also feed on the wood-living ascomycetes associated with recently burned forests. Pyrophilous insects seem to develop in burned forests within 1–5 years after a fire. Some, such as *M. acuminata*, can arrive in swarms at the site of a forest fire within 24 h. Many of these insects are specialists on dead and dying wood, taking advantage of the resources available and the reduced defensive capabilities of the weakened trees. These insects can be crucial to the breakdown of coarse woody debris and post-disturbance nutrient cycling. The reduced competition and warmer microclimate, particularly in boreal forests, may also provide selective pressures for pyrophilous behavior. These insects can develop a specialist community, which contains a range of ecological groups. Because pyrophilous insects can create new communities that include a wide variety of ecological groups, they can provide interesting information about prehistoric fires. For example, the presence of pyrophilous insects in prehistoric forests likely indicates burning of exposed wood rather than burned buried wood within a peat body.

Fire, or fire-suppression, can have effects on the diversity of non-pyrophilous as well as pyrophilous insect species. Fire-induced mortality of ground- and wood-living insects can be substantial, depending on the severity of the fire. However, disturbed forests often show an increase in insect diversity over undisturbed forests. The use of prescribed fire in Finnish boreal forests has been shown to be beneficial for many beetle species, including some threatened ground beetle species. Many insects that are not strictly pyrophilous still depend on the dead trees and decaying wood that result from forest fires. This seems to be particularly true in boreal forests, where fire is one of the most important factors influencing the structural and biological diversity of the forest. As forest management becomes more biodiversity-oriented, management approaches such as green-tree retention (retention of live trees after harvest) and prescribed burning will probably increase in importance. These practices make it possible to imitate the effects of wildfires, creating resources for species that require dead or dying wood, while maintaining some of the structural diversity that is lacking after traditional clear-cutting.

Fire is one of the most important causes of disturbance in forest ecosystems. Pyrophilous insects have evolved complex means of locating recently burned forests, taking advantage of the habitats and resources provided by fire. In addition, many non-pyrophilous insect species benefit from the diverse habitats created by fire. Research on the relationships between fire and insects will remain an exciting area of inquiry for the foreseeable future.

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Pyrrhocoridae

A family of bugs (order Hemiptera). They sometimes are called red bugs or cotton stainers.

► Bugs

Pythidae

A family of beetles (order Coleoptera). They commonly are known as dead log bark beetles.

► Beetles

Pyrrolizidine Alkaloids and Tiger Moths (Lepidoptera: Arctiidae)

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Tiger moths (Arctiidae) are known for their bright aposematic coloration meant to repel predators. Their caterpillars often feed on alkaloid-rich host plants, and it is thought that the noxious substances ingested with the leaves determine the toxicity of both larvae and adults. Laboratory rats die when injected with a dose of arctic alkaloid, and we can safely assume that a natural predator will at least get sick after tasting these brightly colored (and thus memorable) insects, and will avoid eating them in the future. Probably due to these substances, many species of tiger moths were able to become diurnal (daytime) fliers, and many other moths, butterflies, and even beetles form Müllerian mimicry complexes: they all resemble alkaloid-containing arctiid species, so predators should view them all as distasteful.

It has been also suggested that the toxic substances might be synthesized anew by arctiids. In fact, it is the ability of caterpillars to tolerate the noxious compounds secreted for defense against predators that allows them to feed on the toxic plant species (Fig. 136). Indeed, the role of pyrrolizidine alkaloids in the biology of arctiid moths is complex.

The significance of pyrrolizidine alkaloids ingested by the larvae in the reproductive biology of arctiids has been studied extensively. It was shown that alkaloids of the arctiid *Creatonotus gangis* L. influence the morphology and chemistry of coremata (large abdominal hair-covered tubes, which are expanded by a male during the courtship, emitting pheromones). The main compound responsible for the scent can be secreted only when pyrrolizidine alkaloids are present in the larval diet. The size and weight of coremata is also proportional to the amount of alkaloids ingested by the larva.

Pyrrolizidine Alkaloids and Tiger Moths (Lepidoptera: Arctiidae), Figure 136 **Arctiid, *Euchromia collaris*, and noctuid, *Asota* sp., feeding on alkaloid-rich tissues of a Tree Heliotrope, *Tournefortia argentata*. Solomon Islands.**

Numerous brightly colored arctiid moths are attracted to the damaged and wilting tissues of Tree Heliotrope (*Tournefortia argentata*, Boraginaceae), feeding on sap exuded from leaves and branches. Pyrrolizidine alkaloids that are obtained through feeding on the decomposing plant matter by adult butterflies are used to synthesize danaidone, a compound found in the pheromone secretion of the hair-pencil organ in males that serves as a sexual attractant. Hence, one might assume that alkaloids ingested by the adult tiger moths also are used for pheromone production, or at least for boosting their chemical defense against predators. However, research on several tiger moth species in Florida found that moths instead are seeking pyrrolizidine alkaloids as nitrogen-rich nutrients, which they utilize differently depending on their sex. Egg productivity by females who were mated to alkaloid-deprived males was significantly lower than those of females whose mates had a chance to feed on alkaloid-containing plants. Only young males usually feed on pyrrolizidine alkaloids, subsequently passing nutrients with the spermatophore to a female during the copulation. The spermatophore is then stored in the female's bursa copulatrix and is used up gradually. Unlike males, females seek pyrrolizidine alkaloids after they spend several days on the wing. Alkaloids apparently are metabolized by females, enhancing egg production in their nutrient-depleted abdomens. For an unknown reason, only males or only females of each species in Florida feed on the alkaloids, but on the Solomon Islands, either sex of arctiids feed, with mating also occurring at the congregation sites.

The exact reasons for the phenomenon described above is yet to be understood, but it is clear that multiple biochemical mechanisms underlie the attraction of arctiid moths to various alkaloid-containing plants.

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