Insect Diversity

Biological Diversity

- the number and variety of organisms in an ecosystem
- genetic diversity that contributes to population richness

Insect diversity in the world ecosystem

- insects are the most diverse group of organisms
- insects are diverse because of their size and adaptability

To understand diversity, we have to know what is present, the science of **Taxonomy** or **Systematics.**

Traits used to classify insects

- mouthparts
- wings
    - wingless
    - Paleoptera
    - Neoptera
        - exoptergota
        - endoptergota
- genitalia

Insects are classified into about 32 orders and 939 families.

Major Insect Orders

Odonata

Dragonflies and Damselflies

ETYMOLOGY: Means toothed jaw. A name surviving from a classification devised by Fabricius (Danish entomologist and sometimes pupil of Linneaus) that was based on mouthparts rather than wings.

METAMORPHOSIS: Incomplete, hemimetabolous but immature nyaids bear little resemblance to adults.

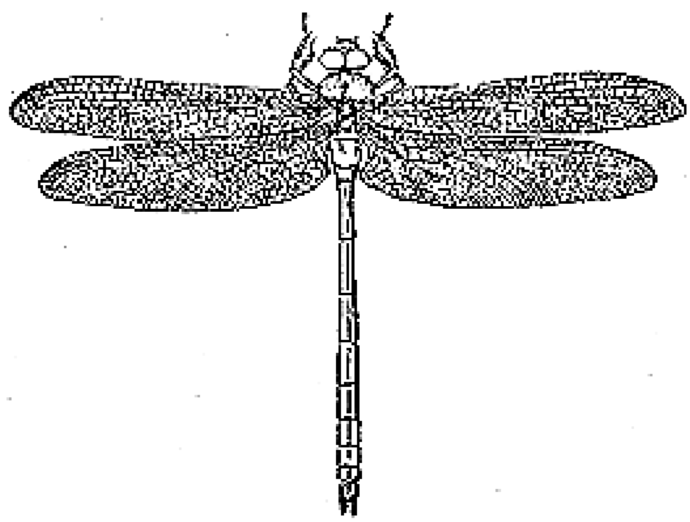
HABITS: Larvae are called nymphs or naiads and are aquatic predators, adults are usually found near water.

IMPORTANCE: Beneficial predators of mosquitoes, gnats, and other flies and insects.

FOLKLORE: Sometimes called the devil's darning needle, if they caught you they would sew up your mouth, nostrils, eyelids, or ears. Snake doctor, thought to guard snakes.

IDENTIFYING CHARACTERS: Two pairs of elongate, membranous wings. Long bodied.

SUBORDER: *Anisoptera* = Dragonflies



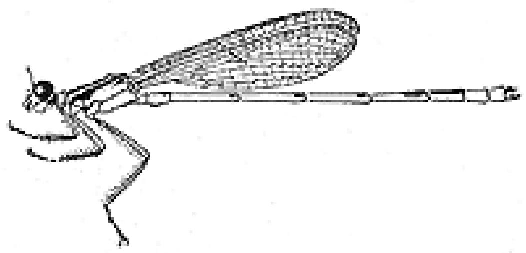
- An unusual insect group. They have extremely acute vision, capture their prey on wing, and are perhaps the best fliers in the animal kingdom. Most strong insect fliers link their fore and hind wings, Odonates do not. The two wing pairs operate separately and provide Odonata with great agility, power, and speed. They have been timed at up to almost 60 mph.
- Identifying Characters:
    - wings at rest held out from the sides of the body
    - usually larger and more robust than damselflies

SUBORDER: *Zygoptera* = Damselflies. Like the dragonflies, damselflies are aerial predators, with extremely good vision. Usually smaller than dragonflies with more delicate bodies.

- Identifying Characters:
    - Wings at rest held together over the back
    - usually smaller than dragonflies

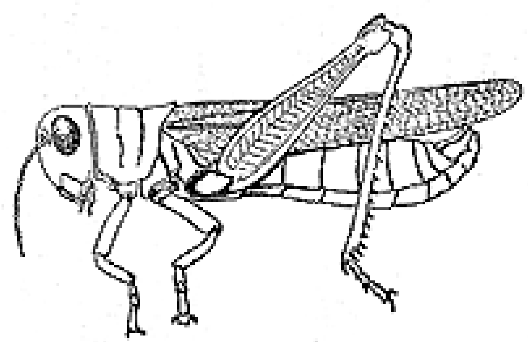
Damselfly

Link to Tree of Life - [Odonata](#)



Orthoptera

Grasshoppers, Crickets, and Katydids



ETYMOLOGY: Straight winged, from *Ortho*- as in orthopedics, orthodox.

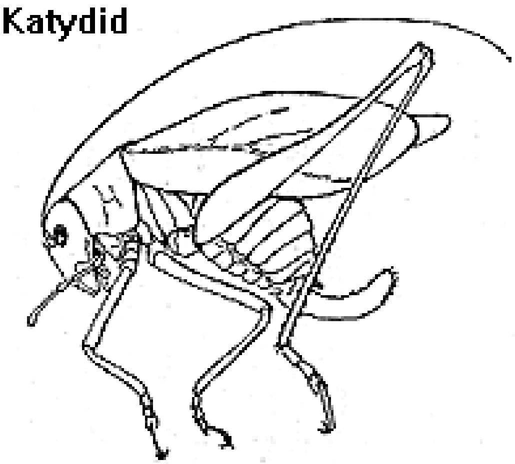
METAMORPHOSIS: Incomplete**.**

HABITS: Terrestrial, phytophagous, many sing by stridulation.

IMPORTANCE: Many economically damaging plant feeders. May migrate in enormous numbers.

FOLKLORE: Katydid - A tale told to children. A little girl named Katy who had told a fib and willfully and stubbornly compounded her error by refusing to say she had lied was struck dead by God. Thereafter, her shame lived on as even the bugs in the trees debated whether Katy did or didn't and if you listen closely you will hear that most of them think she did.

Katydid



Katydid - Another story. A young woman named Katy fell in love with a handsome young man who scorned her and instead married her prettier sister. After the honeymoon, the couple were found dead, poisoned in their bed. And then the bugs began debating whether Katy did or not.

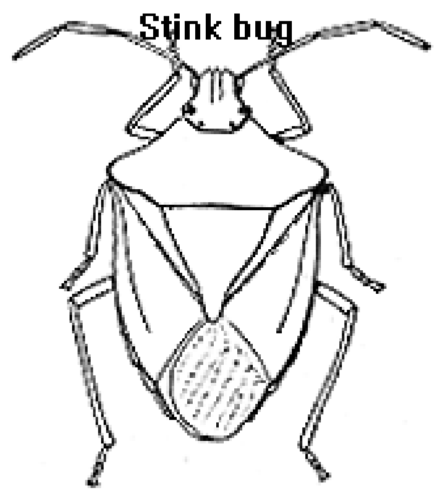
An old English definition of a "katy" is a wanton.

IDENTIFYING CHARACTERS: Most large to medium sized, jumping insects. Usually two pairs of wings with many veins. Forewings usually long, narrow, and leathery; hindwings broad and membranous.

Link to Tree of Life - Orthoptera

Hemiptera

True Bugs



ETYMOLOGY: Half-winged. Most insects in this order have forewings that are divided into two parts. The first or basal part is thickened and leathery looking. The second, or distal part, is delicate and membranous.

METAMORPHOSIS: Incomplete.

HABITS: Varied, terrestrial, freshwater, marine. Phytophagous and predacious.

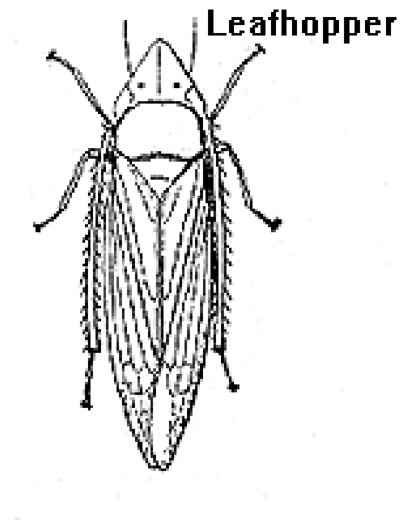
IMPORTANCE: Many economically damaging species, other species are important predators, some disease vectors.

IDENTIFYING CHARACTERS: The basal half of the forewings are thick and leathery, the distal tip is membranous. Characterized by beaked, piercing-sucking mouthparts.

Link to Tree of Life - Hemiptera

Homoptera

Aphids, Leafhoppers, Planthoppers, Scales, and Cicadas



ETYMOLOGY: Whole-winged. Both wings membranous.

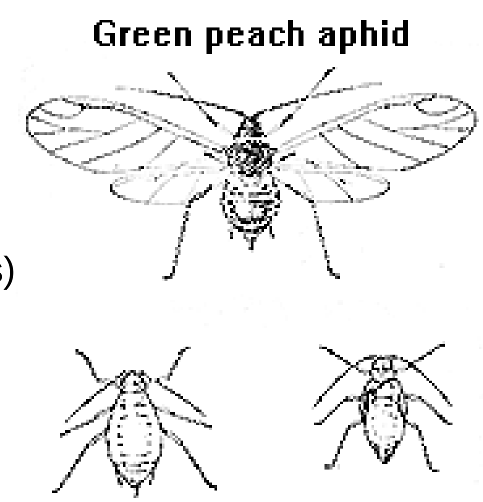
METAMORPHOSIS: Incomplete.

HABITS: Terrestrial plant feeders.

IMPORTANCE: Many economically damaging species, some vector plant diseases.

IDENTIFYING CHARACTERS: Mouthparts like the Hemiptera but short and arising from the back of the head, often appearing to arise from between the first pair of legs. Two pair of membranous wings. Some without wings.

Green Peach Aphid (Winged Adult and Nymphs)



Link to Tree of Life - Heteroptera (True Bugs)

Coleoptera

Beetles

ETYMOLOGY: *Koleon* (Greek) - a sheath

METAMORPHOSIS: Complete

HABITS: Largest order of insects, terrestrial and aquatic, predacious, phytophagous, and scavengers.

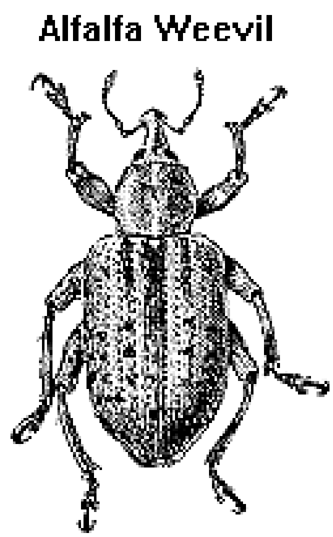
IMPORTANCE: Many important predacious and plant feeding species.

FOLKLORE:

> The firefly is a funny bug.
> He hasn't any mind. He blunders all
> the way through life.
> With his headlight on behind.

From the poems of A. Nony Mouse (Jack Prelutsky**)**

IDENTIFYING CHARACTERS: Forewing hardened into a protective covering, the elytra, that encloses the delicate flying wings which are folded underneath it when not in use.



The largest insect group. Both the largest and smallest insects are beetles.

Link to Tree of Life - Coleoptera

Lepidoptera

Butterflies, Skippers, and Moths

ETYMOLOGY: *Lepis* (Greek) scales, scaly-winged

METAMORPHOSIS: Complete

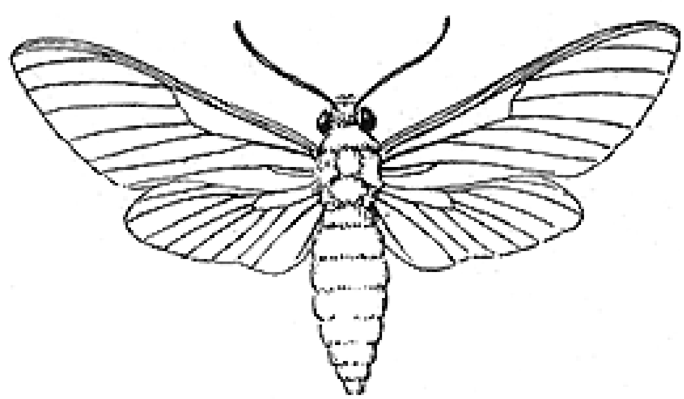
HABITS: Terrestrial. Adults feed on nectar and other liquid food, most larvae are phytophagous.

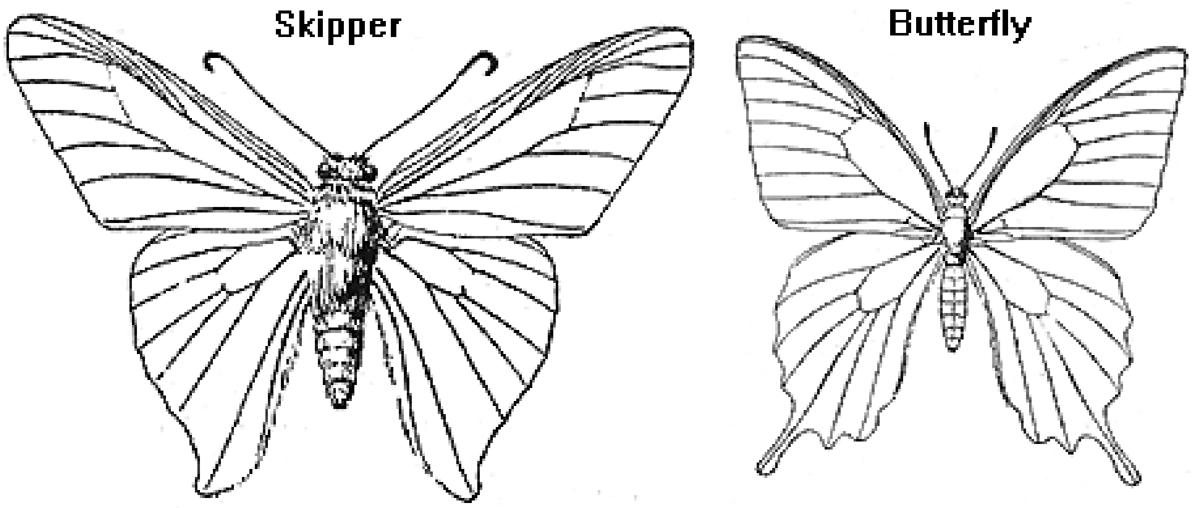
IMPORTANCE: Many economically damaging species of crops, stored food, and fabrics.

IDENTIFYING CHARACTERS:

Groups	Antennae	Active Period	Pupal Chamber	Body	Wing Position at Rest
Moths	Feathery	Night	Cocoon	Stout	Roof-like or against body
Skippers	Hooked	Day	Cocoon	Somewhat stout	Two wings at different angles
Butterflies	Clubbed	Day	Chrysalis	Slender	Vertically above body

Moth



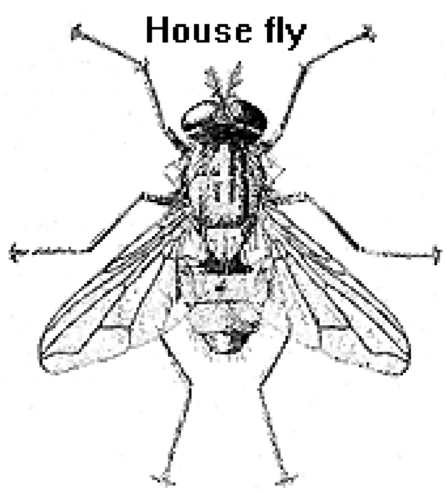


LINKS:

- to Electronic Resources on Lepidoptera
- to Tree of Life - Lepidoptera
- American Museum of Natural History Butterfly Expedition

Diptera

Flies, Mosquitoes, and Gnats



ETYMOLOGY: *Dis* (Greek) twice, two-winged.

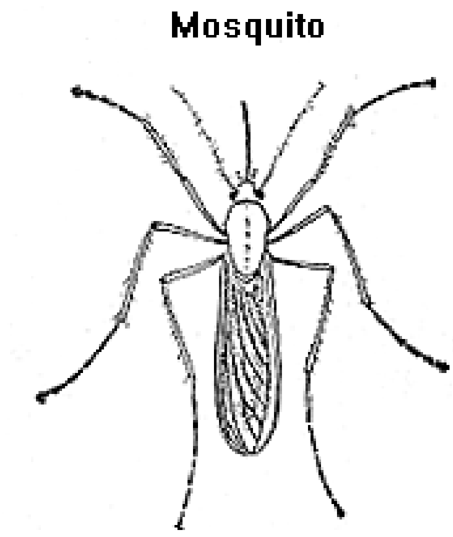
METAMORPHOSIS: Complete.

HABITS: Aquatic, terrestrial, found almost everywhere.

IMPORTANCE: Many predacious and parasitic species, vectors of diseases such as sleeping sickness, malaria, yellow fever, dengue fever, elephantiasis, encephalitis. Many nuisance species. Some are plant pests or vector plant diseases.

FOLKLORE: Two of the 10 plagues of ancient Egypt were flies. Ancient Semitic deity, Beelzebub, was the "Lord of Flies". People thought that Beelzebub would protect them from flies.

IDENTIFYING CHARACTERS: Single pair of flying wings, the second pair of wings as little knobs called halteres.

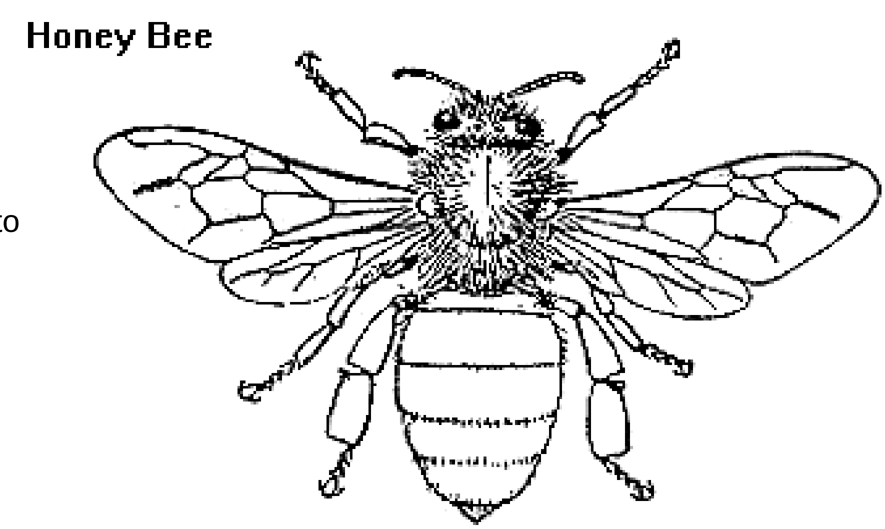


Mosquito

Link to Tree of Life - Diptera

Hymenoptera

Bees, Ants, Wasps and Sawflies



ETYMOLOGY: Membrane winged.

METAMORPHOSIS: ***Complete.***

HABITS: Terrestrial from the Arctic to the tropics. Some social groups and species. Ovipositor modified into a sting.

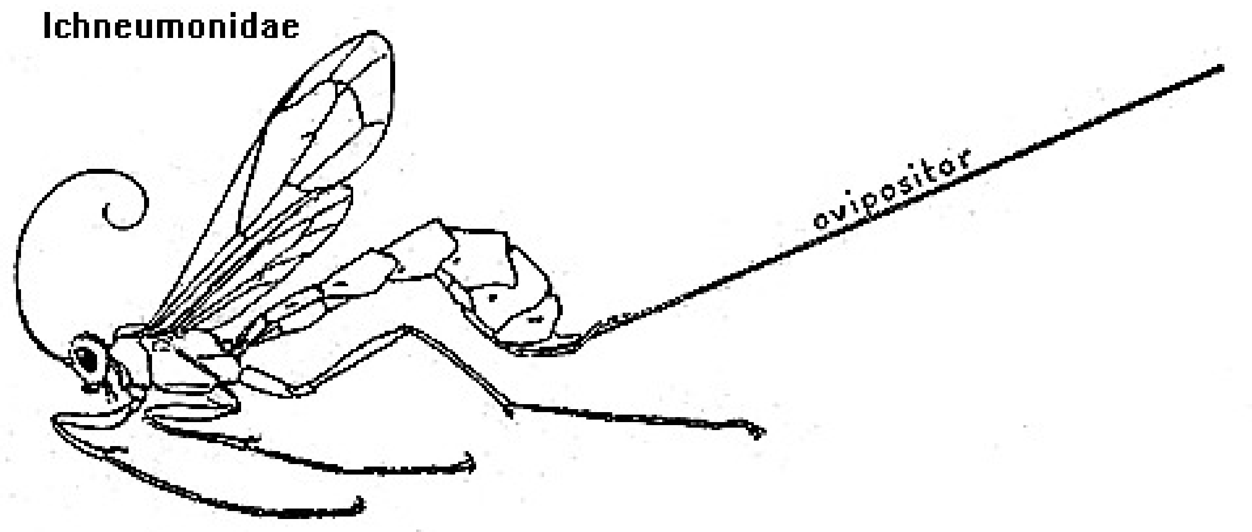
IMPORTANCE: Great significance as pollinators, predators, and as parasitoids. Some economically damaging species.

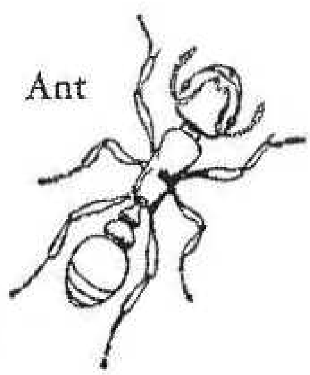
FOLKLORE: "The Ant and the Grasshopper" by Aesop extols the virtues of hard work and preparation. Bees are industrious.

- Considered wise, references in the bible and other sources. Ants are considered great teachers, from Proverbs, "None teaches better than the ant, and she says nothing."

- Associated with fidgeting, "have ants your pants."

IDENTIFYING CHARACTERS: Wings, if present, are membranous. Chewing mouthparts. Except for sawflies, base of abdomen constricted, may be distinctly thread-like.





Link to Tree of Life - Hymenoptera

Links to Related Entomological Sites

- On-line Insect Database at the University of Delaware's College of Agriculture
- Wonderful World of Insects, click on classification at the top of the page
- Tree of Life - Insecta at the University of Arizona

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Last updated Dec. 30, 2000
Gary Brewer

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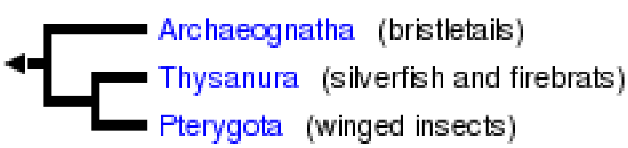
Insecta

Insects



Containing group: [Hexapoda]

Characteristics

Insects have a large number of unique, derived characteristics, although none of these are externally obvious in most species. These include (Kristensen, 1991):

- lack of musculature beyond the first segment of antenna.

- Johnston's organ in pedicel (second segment) of antenna. This organ is a collection of sensory cells that detect movement of the flagellum.
- a transverse bar forming the posterior tentorium inside the head
- tarsi subsegmented
- females with ovipositor formed by gonapophyses from segments 8 and 9
- annulated, terminal filament extending out from end of segment 11 of abdomen (subsequently lost in most groups of insects)

Discussion of Phylogenetic Relationships

The relationships of primitively wingless insects to each other and to winged insects (pterygotes) is well established, with a few exceptions.

One notable feature linking Thysanura + Pterygota is the presence of two articulations on each mandible. Archaeognathans have only one mandibular condyle or articulation point; they are "monocondylic". Thysanura + Pterygota, with their two mandibular condyles, are sometimes called Dicondylia. The many other apomorphies linking Dicondylia are described in Kristensen (1991).

It is possible that the thysanurans are not themselves monophyletic; Thysanura (exclusive of the family Lepidothricidae) plus pterygotes may be monophyletic, with lepidothricids sister to this complex (Kristensen, 1991).

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  - Entomology Databases.
- Entomology Department of Harvard's Museum of Comparative Zoology
  - MCZ Entomology Primary Type Specimen Database.
- Entomology Department. California Academy of Sciences.
- The Essig Museum of Entomology. Berkeley, California.
- Insect Division. University of Michigan Museum of Zoology.
- Bishop Museum Hawaii Entomology Home
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- Introduction to Insect Biology & Classification. The University of Queensland.
- Virtual Exhibit on Canada's Biodiversity: Insects.
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- Compendium of Hexapod Classes and Orders. North Carolina State University.
- Nomina Insecta Nearctica. A Checklist of the Insects of North America.
- Common Names of Insects in Canada. Entomological Society of Canada.
- The Canadian National Collection (CNC) of Insects, Arachnids and Nematodes.
- Singing Insects of North America. By Thomas J. Walker (crickets and katydids) and Thomas E. Moore (cicadas).
- Entomology Database KONCHU. Species Information Database on Japanese, East Asian and Pacific Insects, Spiders and Mites.
- A Catalogue of the Insects of South Africa.
- CSIRO Entomology Home Page.
- General Entomology Resources from Scientific Reference Resources:
  - Entomology Events Calendar.
  - Directory of Entomology Departments and Institutes (DEDI).
  - Directory of Entomological Societies.
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- Entomology Index of Internet Resources. Iowa State University.
- Entomology on the WWW. Colorado State University.
- Entomology on the WWW. Michigan State University.
- BIOSIS BiologyBrowser: Insecta.

Images and Other Media:

- Hawaiian Insect Image Galleries. Bishop Museum.

- Entomology Image Gallery. Iowa State University.
- Very Cool Bugs.
- Dennis Kunkel's Microscopy.
- The Virtual Insectary.
- Thais in 2000: Entomology.
- Reference Library of Digitized Insect Sounds. Richard Mankin, Center for Medical, Agricultural and Veterinary Entomology, Gainesville, Florida.

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- Eocene Fossils.
- Fossil insects from Florissant (Colorado). Peabody Museum of Natural History.
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- Nature's Preservative--Organic Flypaper: Amber Gives a Green Light to Study of Ancient Life. The Why files. University of Wisconsin.
- Amber Home. Gary Platt.
- Baltic Amber Inclusions. Wolfgang Wiggers.
- Dominican Amber Fossils. ESP Designs.
- The Amber Room. Steve Kurth.

Famous entomologists:

- Thomas Say (1787-1834), father of American entomology.
- Charles Darwin (1809-1882), AboutDarwin.com.
- Jean-Henri Fabre (1823-1915) e-museum.
- Famous Entomologists on Postage Stamps.

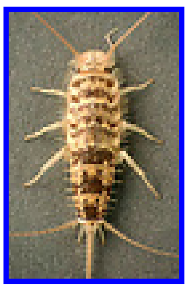
For young entomologists:

- bugbios. Shameless promotion of insect appreciation by Dexter Sear.
- O. Orkin Insect Zoo. National Museum of Natural History. Smithsonian Institution.
- Bug Camp. Field Museum of Natural History, Chicago.
- Insectclopedia. Links to websites about insects.

- Bugscope. Educational outreach project of the World Wide Laboratory.
- The Bug Club for Young Entomologists. UK Amateur Entomologists' Society.
- The Wonderful World of Insects.
- Class: Insecta. Spencer Entomological Museum at the University of British Columbia, Vancouver, Canada.

Title Illustrations

Scientific Name	Machilidae
Location	USA: North Carolina: Durham
Comments	Bristletail (Archaeognatha)
Specimen Condition	Live Specimen
Copyright	© 2004 David R. Maddison



Scientific Name	Thermobia domestica
Location	Tucson, Arizona, USA
Comments	Silverfish (Thysanura)
Copyright	© 2003 David R. Maddison

Scientific Name	Zygoptera
Location	Zion National Park (Utah, USA)
Comments	Narrow-winged damsel fly (Pterygota)

Creator	Photograph by Robert Potts
Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
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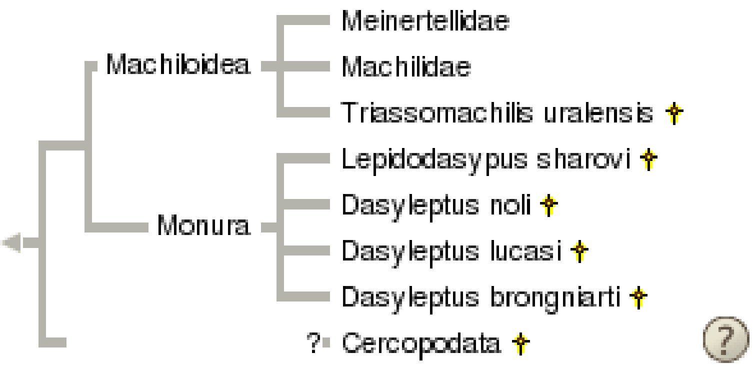
Archaeognatha

Bristetails



Tree after Bitsch & Nel (1999) and Rasnitsyn (1999).
Containing group: Insecta

Introduction

This order of wingless insects consists of about 350 known species. They hide under bark, in litter, and in rock crevices, and feed on algae, lichens, and vegetable debris.

Oldest fossil considered as Archaeognatha is from the Devonian (390 million years old) from Gaspé, Québec (Labandeira et al., 1988). However, there is little evidence that this fossil is a member of Archaeognatha; it may instead be a member of the stem-group of insects or of stem-Dicondylia.

Characteristics

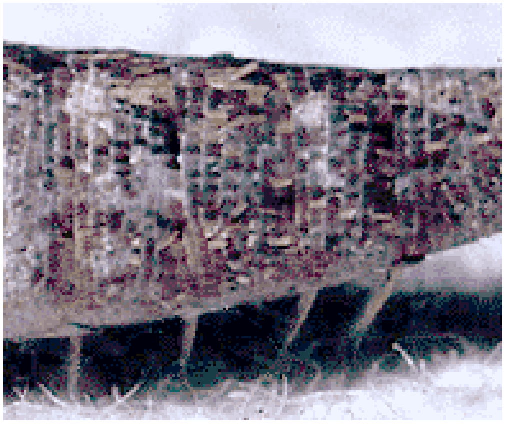
Recent archaeognathans share two notable derived features:

- Compound eyes enlarged, medially contiguous

- Specialized musculature of abdomen, which allows them to jump by a rapid downward bending

Archaeognathans also share a number of primitive features. Their mandibles are monocondylic, that is, with only one condyle (the joint or socket-like attachement point to the head capsule), whereas other insects have two condyles ("dicondylic"). This primitive mouthpart feature gives the order its name (Arche - beginning, gnathos - jaw).

Their abdominal segments bear styles, which are small appendages moveable by muscles. They can be seen underneath the abdomen in the following picture:



Styli may be remnants of ancestral limbs.

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- The Bristletails (Archaeognatha) of South Africa. Compiled by John Irish, National Museum, Bloemfontein, South Africa.
- Nomina - Archaeognatha. nearctica.
- California Academy of Sciences Archaeognatha Type Collection.

Title Illustrations

Scientific Name	Archaeognatha
Location	USA: North Carolina: Durham
Specimen Condition	Live Specimen
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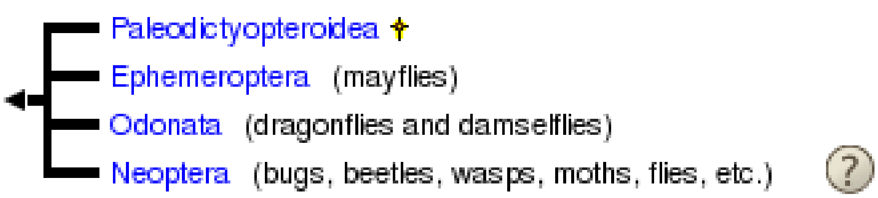
  - Paleodictyopteroidea

Pterygota

Winged insects





Containing group: Insecta

Introduction

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Winged insects, or pterygotes, have radiated into over 100 times more species than all of the winged vertebrate lineages combined. They include all of the commonly encountered insects; the most common non-pterygote insect lineage are the Thysanura (silverfish and firebrats).

Many groups of insects have subsequently lost the ability to fly. Some of these (lice and fleas, for example) have lost all remnants of wings. It is only through their evident relationship with particular groups of winged insects (lice are closely related to psocids [book lice]; fleas are related to flies) that it is clear that their ancestors had wings.

Characteristics

The primary derived characteristic of pterygotes is the presence of veined wings on the second (meso-) and third (meta-) thoracic segment.

Paleopterous and neopterous insects

Two groups of pterygotes evolved the ability to fold their wings back flat against their abdomens. The largest of these is the clade Neoptera ("new wing"). Remaining insects (all of the taxa in the above tree except for Neoptera) are sometimes referred to as Paleoptera ("old wing"), because they lack the sophisticated wing-folding mechanism of neopterous insects. Members of paleopterous insects cannot fold their wings back over their abdomens, with the exception of the extinct order Diaphonopterodea, which could fold their wings using a mechanism different than Neoptera. (Some neopterous insects, such as butterflies, can no longer fold their wings against their abdomen, but this clearly represents a secondary loss.)

Discussion of Phylogenetic Relationships

While the relationships of the extinct paleodictyopteroid orders (Diaphanopterodea, Paleodictyoptera, Megasecoptera, and Permothemistida) to each other and to other orders have not been extensively examined, the relationships of the three living lineages (Ephemeroptera, Odonata, and Neoptera) to each other have been the subject of much debate. Each of the three possible relationships are supported by various authors.

A monophyletic Paleoptera was advocated by Hennig (1969, 1981) and Hovmöller et al. (2002):

```
                        === Odonata
```

```
     ==Paleoptera=|
=====|            === Ephemeroptera
     |
     ================ Neoptera
```

Boudreaux (1979) favored monophyly of Ephemeroptera + Neoptera:

```
     ====== Odonata
     |
=====|  === Ephemeroptera
     ===|
        === Neoptera
```

Kristensen (1975, 1981, 1991) and Wheeler et al. (2001) present evidence in support of monophyly of Odonata + Neoptera:

```
     ====== Ephemeroptera
     |
=====|  === Odonata
     ===|
        === Neoptera
```

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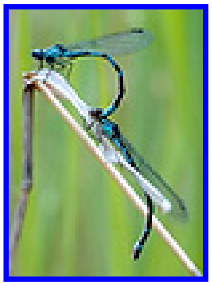
Information on the Internet

- The Development of Insect Flight

Title Illustrations

Scientific Name	Ephemeroptera
Location	McKinleyville (Humboldt County, California, USA).
Comments	A mayfly (Ephemeroptera)
Creator	Photograph by T. W. Davies

Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
Copyright	© 1999 California Academy of Sciences



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Location	Pepperwood (Sonoma County, California, USA)
Comments	A pair of damselflies
Creator	Photograph by Jo-Ann Ordano
Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
Copyright	© 2000 California Academy of Sciences

Scientific Name	Plusiotis beyeri
Comments	Beyer's scarab beetle
Creator	Photograph by Robert Potts
Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
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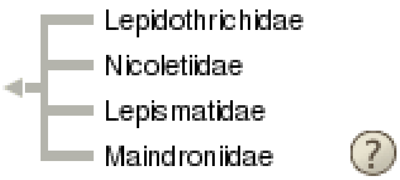
Thysanura

Silverfish and Firebrats



Containing group: [Insecta]

Introduction

Under bark, litter, caves, ant nests, deserts, etc. Omnivorous. 4 Families (3 in North America), 370 Species (in North America)

Oligocene to Recent. Lepidotrichidae more widespread in early deposits than currently.

Characteristics

Characteristics:

- body flattened
- long cerci and median filament
- compound eyes separate

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Information on the Internet

- Checklist of the Thysanura of South Africa
- Nomina Insecta Nearctica - Thysanura

Title Illustrations

Scientific Name	Thermobia domestica
Location	Tucson, Arizona, USA
Specimen Condition	Live Specimen
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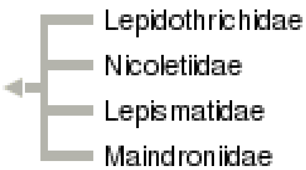
Thysanura

Silverfish and Firebrats



Containing group: [Insecta]

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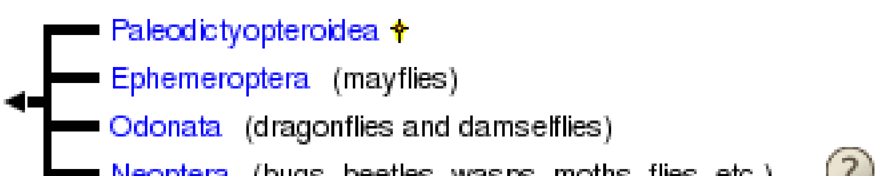
Pterygota

Winged insects



Containing group: Insecta

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Two groups of pterygotes evolved the ability to fold their wings back flat against their abdomens. The largest of these is the clade Neoptera ("new wing"). Remaining insects (all of the taxa in the above tree except for Neoptera) are sometimes referred to as Paleoptera ("old wing"), because they lack the sophisticated wing-folding mechanism of neopterous insects. Members of paleopterous insects cannot fold their wings back over their abdomens, with the exception of the extinct order Diaphonopterodea, which could fold their wings using a mechanism different than Neoptera. (Some neopterous insects, such as butterflies, can no longer fold their wings against their abdomen, but this clearly represents a secondary loss.)

Discussion of Phylogenetic Relationships

While the relationships of the extinct paleodictyopteroid orders (Diaphanopterodea, Paleodictyoptera, Megasecoptera, and Permothemistida) to each other and to other orders have not been extensively examined, the relationships of the three living lineages (Ephemeroptera, Odonata, and Neoptera) to each other have been the subject of much debate. Each of the three possible relationships are supported by various authors.

A monophyletic Paleoptera was advocated by Hennig (1969, 1981) and Hovmöller et al. (2002):

```
                  === Odonata
```

```
     ==Paleoptera=|
=====|            === Ephemeroptera
     |
     ================ Neoptera
```

Boudreaux (1979) favored monophyly of Ephemeroptera + Neoptera:

```
     ====== Odonata
     |
=====|  === Ephemeroptera
     ===|
        === Neoptera
```

Kristensen (1975, 1981, 1991) and Wheeler et al. (2001) present evidence in support of monophyly of Odonata + Neoptera:

```
     ====== Ephemeroptera
     |
=====|  === Odonata
     ===|
        === Neoptera
```

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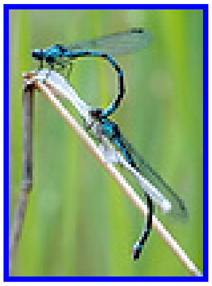
Information on the Internet

- The Development of Insect Flight

Title Illustrations

Scientific Name	Ephemeroptera
Location	McKinleyville (Humboldt County, California, USA).
Comments	A mayfly (Ephemeroptera)
Creator	Photograph by T. W. Davies

Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
Copyright	© 1999 California Academy of Sciences



Scientific Name	Zygoptera
Location	Pepperwood (Sonoma County, California, USA)
Comments	A pair of damselflies
Creator	Photograph by Jo-Ann Ordano
Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
Copyright	© 2000 California Academy of Sciences

Scientific Name	Plusiotis beyeri
Comments	Beyer's scarab beetle
Creator	Photograph by Robert Potts
Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
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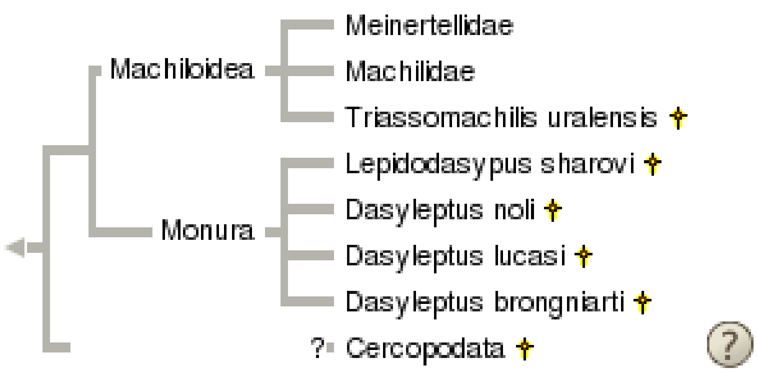
Archaeognatha

Bristetails



Tree after Bitsch & Nel (1999) and Rasnitsyn (1999).
Containing group: Insecta

Introduction

This order of wingless insects consists of about 350 known species. They hide under bark, in litter, and in rock crevices, and feed on algae, lichens, and vegetable debris.

Oldest fossil considered as Archaeognatha is from the Devonian (390 million years old) from Gaspé, Québec (Labandeira et al., 1988). However, there is little evidence that this fossil is a member of Archaeognatha; it may instead be a member of the stem-group of insects or of stem-Dicondylia.

Characteristics

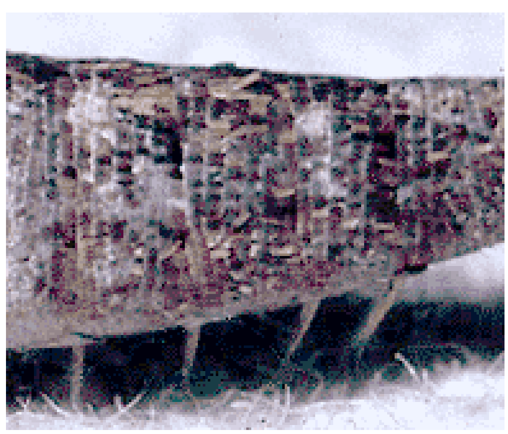
Recent archaeognathans share two notable derived features:

- Compound eyes enlarged, medially contiguous

- Specialized musculature of abdomen, which allows them to jump by a rapid downward bending

Archaeognathans also share a number of primitive features. Their mandibles are monocondylic, that is, with only one condyle (the joint or socket-like attachement point to the head capsule), whereas other insects have two condyles ("dicondylic"). This primitive mouthpart feature gives the order its name (Arche - beginning, gnathos - jaw).

Their abdominal segments bear styles, which are small appendages moveable by muscles. They can be seen underneath the abdomen in the following picture:



Styli may be remnants of ancestral limbs.

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- Nomina - Archaeognatha. nearctica.
- California Academy of Sciences Archaeognatha Type Collection.

Title Illustrations

Scientific Name	Archaeognatha
Location	USA: North Carolina: Durham
Specimen Condition	Live Specimen
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Ephemeroptera

Mayflies

- Schistonota
  - Baetoidea
    - Siphlonuridae
    - Baetidae
    - Oniscigastridae
    - Ameletopsidae
    - Ametropodidae
  - Heptagenioidea
    - Coloburiscidae
    - Oligoneuriidae
    - Isonychiidae
    - Heptageniidae
  - Leptophlebioidea
    - Leptophlebiidae
  - Ephemeroidea
    - Behningiidae
    - Potamanthidae
    - Euthyplociidae

        - Polymitarcydae
        - Ephemeridae
        - Palingeniidae
- Pannota
    - Ephemerelloidea
        - Ephemerellidae
        - Leptohyphidae
        - Tricorythidae
    - Caenoidea
        - Neoephemeridae
        - Baetiscidae
        - Caenidae
        - Prosopistomatidae

Classification from Peters and Campbell (1991), in Insects of Australia.
Containing group: Pterygota

Introduction

Adults do not eat. Immatures are aquatic, feeding on diatoms, algae, or are carnivores.

Carboniferous to Recent.

Ephemeros - short-lived, pteron - wing, referring to the short life span of adults.

Characteristics

Derived characteristics:

- Fore legs of male elongated, used to grasp female in flight.
- mouthparts of adults reduced, unsclerotised.
- hind wings reduced, smaller than fore wings.

In addition, mayflies moult after they have fully-formed, functional wings. Presence of a winged, pre-adult stage ("subimago") is unique among insects.

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    - Mayflies of Central America.
- EphemeropteraGalactica. Florida A&M University.
- Mayflies of the United States. Coordinated by Boris C. Kondratieff. USGS Northern Prairie Wildlife Research Center.
- Ephemeroptera Germanica. Arne Haybach, Mainz.
- Ephémères de France. Gérard Masselot.
- The Mayflies (Ephemeroptera) of South Africa. Compiled by Helen Barber-James.
- Ephemeroptera Types in the Former USSR.

Title Illustrations

Scientific Name	Hexagenia sp.
Location	Kansas City, Kansas, USA
Comments	Yellow Drake Mayfly
Specimen Condition	Live Specimen
Copyright	© 2003 Alex Wild

Scientific Name	Ephemeroptera
Location	Washoe Co., Nevada, U.S.A.
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Copyright	© 2004 Alex Wild

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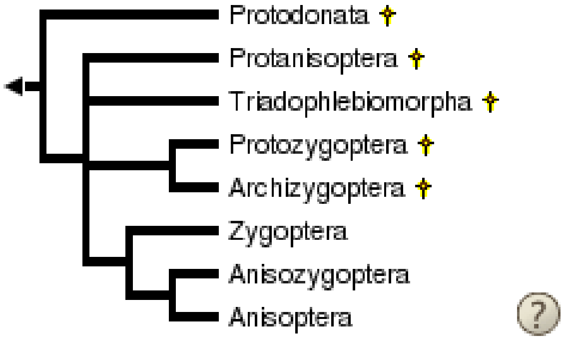
Odonata

Dragonflies and damselflies

John W. H. Trueman and Richard J. Rowe



Containing group: Pterygota

Introduction

Odonata are an order of aquatic palaeopterous insects. There are about 6500 extant species in just over 600 genera. Adult odonates are medium to large in size, often conspicuous and/or brightly colored insects and are aerial predators hunting by sight. They generally are found at or near fresh water although some species roam widely and may be found far from their breeding sites. The larvae are predatory, aquatic and occur in all manner of inland waters.

In some countries, notably Japan, Odonata have long been a popular subject of art and culture, and rank with butterflies and birds as a topic of popular scientific interest. In the European folk tradition, odonates are generally accorded a less favourable status as "horse-stingers" or "devil's darning needles". In fact they neither sting nor bite and all species are completely harmless. If anything, Odonata are beneficial to humans because as voracious aquatic predators they assist in the control of insect pests.

To some extent the presence of odonates may be taken as an indicator of ecosystem quality. Local faunal composition may be strongly affected by any change in water flow, turbidity, etc., or in aquatic or waterside vegetation. The greatest numbers of species are found at sites which offer a wide variety of microhabitats.

Inland fishermen may know dragonfly larvae as "mud-eyes" and use them as bait. Adult dragonflies are a minor food item in some countries, and the larvae sometimes have been used to control pest insects (eg, mosquitos in domestic water tanks). But, for the most part, Odonata are of little economic importance. Their main attraction for humans is aesthetic.

The modern order is divided into two main suborders: Zygoptera (damselflies) and Anisoptera (dragonflies). The common name "dragonfly" also is used for the whole order. More than one-half of all species are tropical but odonates of both major suborders occur in every faunal region except Antarctica. A third suborder, Anisozygoptera, largely known from fossils, is represented by one extant species in Japan and one in the Himalayas.

Sympetrum corruptum. USA. Anisoptera; family Libellulidae. Photo: Larry J. Friesen

Epiophlebia superstes. Japan. Anisozygoptera; family Epiophlebiidae, emergent adult on its larval skin. Photo: Takashi Aoki

Superfamily and family distributions in Odonata reflect ancient vicariance events such as the break-up of the southern continent Gondwana. Some genera and species are widespread. Others are highly local in distribution. Some families are restricted to cool streams or rivers, others to ponds or other still waters, and some to marshy places. The most species-rich and widespread family is the mainly tropical Libellulidae (Anisoptera). The most restricted is the monotypic Hemiphlebiidae (Zygoptera), only known from six or so small reedy pools in south-eastern Australia.

The fossil record for most modern families dates back to the Jurassic or else the Cretaceous period. Fossil species not assignable to any of the the three extant suborders are placed conventionally into one of four fossil suborders: Protozygoptera, Archizygoptera, Protanisoptera and Triadophlebiomorpha. A separate order, Protodonata, occasionally regarded as a suborder of Odonata, contains some very large to enormous Upper Carboniferous and Permian fossil odonatoid species. The largest of these "giant dragonflies", Meganeuropsis permiana, measured about 720 mm from wingtip to wingtip. The wingspan of modern anisopterans ranges from less than 20 mm (eg, Nannodiplax rubra, Libellulidae) to more than 160 mm (eg, Petalura ingentissima, Petaluridae): those of modern Zygoptera range from about 18 mm (eg, Agriocnemis pygmaea, Coenagrionidae) to about 190 mm (Megaloprepus caerulatus, Pseudostigmatidae).

Characteristics: adults

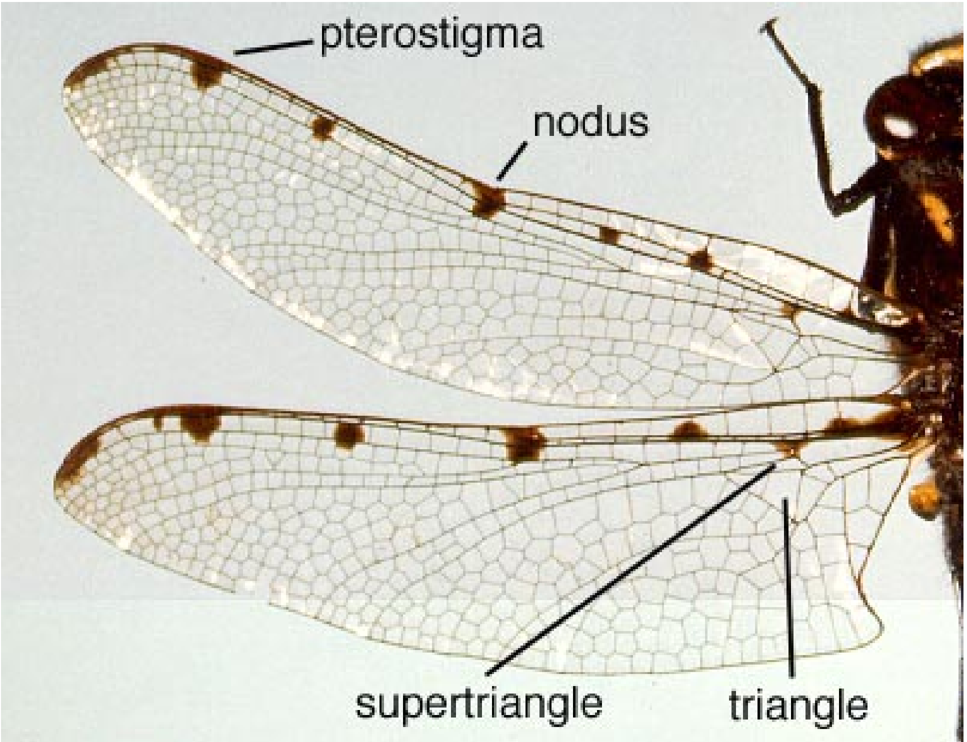
General: The head is large, concave behind, on a flexible neck. The compound eyes are large and either widely separated (all Zygoptera, some Anisoptera), just touching, or extensively fused along the mid-line. The face carries three ocelli and a pair of short, bristle-like antennae. The prothorax is small, the mesothorax and metathorax are large and fused into a single, strong pterothorax. The legs are weak, suited to perching and to holding prey but not to walking. The abdomen is long, rarely any shorter than the length of one wing, and flexible, with 10 visible segments, and terminates in clasping organs in both sexes. In Zygoptera the abdomen almost always is thin and cylindrical. Females of all zygopteran and several anisopteran families carry a prominent ovipositor under abdominal segments 9-10. Males always possess secondary genitalia on the underside of abdominal segments 2-3.

Resting attitude: The wing veins of Odonata are fused at their bases and the wings cannot be folded over the body at rest. Almost all Anisoptera settle with the wings held out sideways or slightly downward. Most Zygoptera settle with the wings held together, dorsal surfaces apposed. However, the zygopteran thorax is so oblique that when held in this way the wings fit neatly along the top of the abdomen. They do not appear to be held straight 'up' as in butterflies or mayflies. In a few zygopteran families the wings are held horizontally at rest, and in one anisopteran genus (Cordulephya, Corduliidae) the wings are held in the typical damselfly resting position.

Wing venation: Adult Odonata possess two pairs of equal or subequal wings. There appear to be only five main vein stems. A Nodus is formed where the second main vein (subcosta) meets the leading edge of the wing. In most families a conspicuous pterostigma is carried near the wing tip.

Identification as Odonata can be based on the venation. The only likely confusion is with some lacewings (order Neuroptera) which have many crossveins in the wings. Until the early years of the 20th century Odonata were often regarded as being related to lacewings and were given the ordinal name Paraneuroptera, but any resemblance between these two orders is entirely superficial.

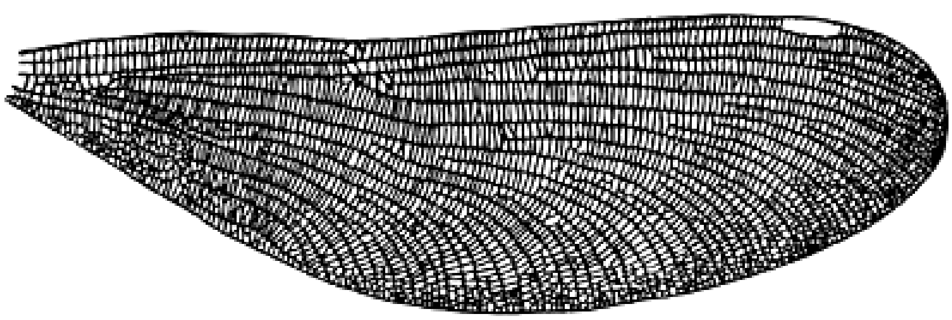
In Anisoptera the hindwing is broader than the forewing and in both wings a crossvein divides the discoidal cell into a Triangle and Supertriangle.



Wings of *Archipetalia auriculata* (Neopetaliidae) *taxonomic note
Photo: J. W. H. Trueman, Copyright © 1997 J. W. H. Trueman

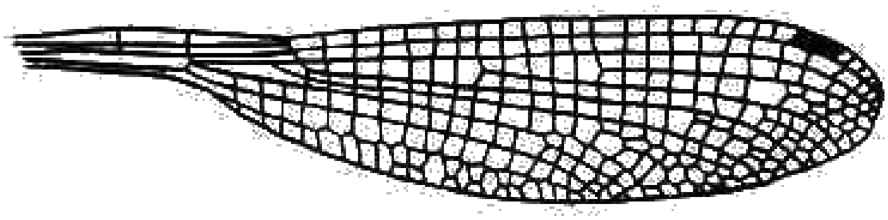
Rarely, the crossvein runs obliquely across the cell, causing either the Triangle or Supertriangle to appear four-sided.

In Zygoptera the two pairs of wings are almost exactly equal in shape, size and venation. There may be very numerous crossveins:



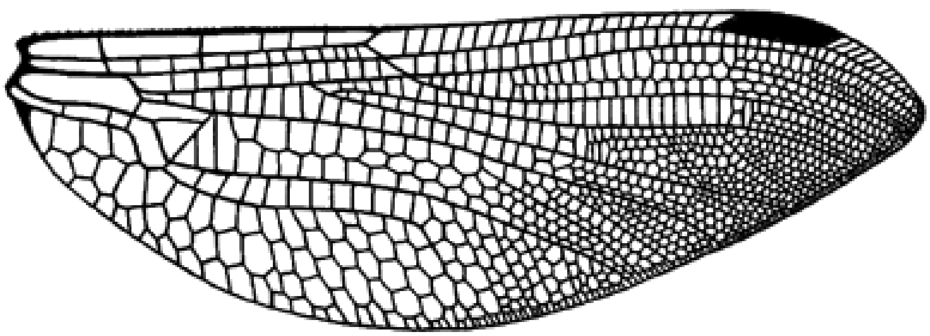
Hindwing venation of *Matrona japonica* (Calopterygidae).

or rather few:



Hindwing of *Austroargiolestes icteromelas* (Megapodagrionidae).

The venation in Anisozygoptera is intermediate between that of the two major suborders:



Hindwing venation of Jurassic fossil species *Heterophlebia buckmani*.

Characteristics: larvae

The most obvious characteristic shared by all odonate larvae is a conspicuous grasping labium (lower lip: mask), used for capturing prey.

At rest the mask is held folded underneath head and thorax, extending back as far or further than the front legs and in some families far enough forward to cover the face below the compound eyes. In prey capture the labium is shot rapidly forward and prey is grasped with paired, hand-like palps.

Even from above and with the mask retracted, identification of larvae to order and suborder is very easy, based on several other features.

Life Cycle and Behavior

Odonate larvae are non-discriminate hunters which will eat any animal as large as or smaller than themselves, including their own species. Small vertebrates such as tadpoles and fish fry are not immune from attack. Prey may be stalked or ambushed. Captured prey is pulled back using powerful muscles in the labium and chewed by strong mandibles. More details on labium structure and larval predatory activity are available.

Almost all odonate larvae are aquatic. They occur in every sort of water body from soaks and seepages to streams and rivers, lakes, temporary pools and water-filled tree holes. A few species tolerate moderate salinity, a few others have semi-terrestrial larvae which roam across the surface of bogs and swamps at night. A half-dozen or so fully terrestrial larvae are known from distantly related families.

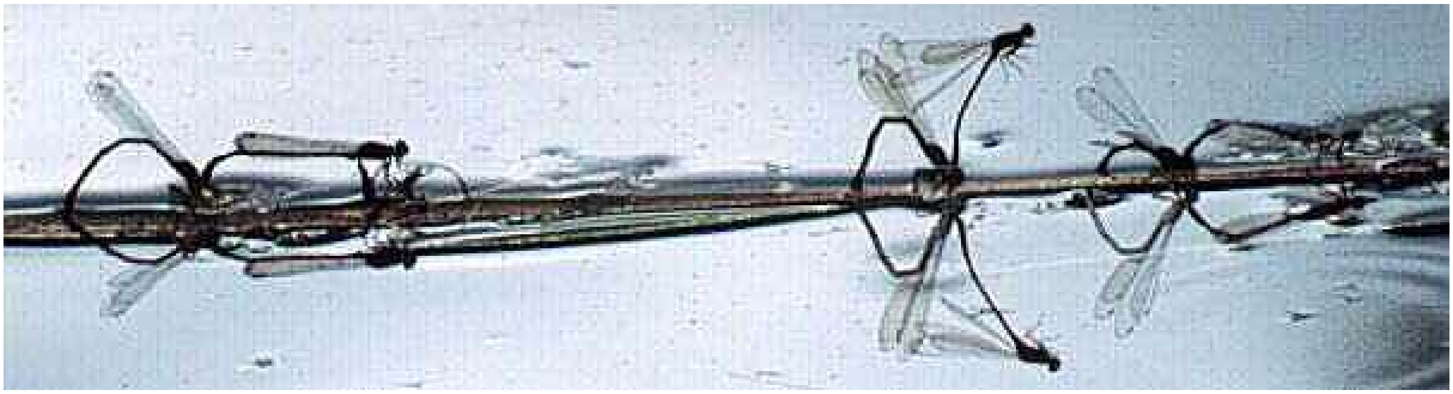
As they grow, larvae undergo approximately 10-20 molts, over a time between 3 months and about 6-10 years depending on species. Instar number is not always fixed but may depend on seasonal conditions and food supply. Wing pads develop externally from about the 6-7th instar. Metamorphosis is direct without a pupal stage and emergence takes place on a fixed support out of the water, sometimes a considerable distance from the water's edge. The newly emerged adult flies away from water for a few days to feed and mature, during which time the full adult color develops. Teneral (new) adults can be recognised by a glassy sheen of the wings. Additional color changes occur later in life in some species.

Adult Odonata are visually oriented hunters with exceptional aerobatic ability and extremely acute eyesight. Many are strong fliers, and to catch them can be extremely difficult. Males tend to congregate around the breeding sites where they may be seen either perched on waterside vegetation, hovering over small territories or hawking up and down in search of females. Females of many species spend much time away from the water, only appearing to mate and lay eggs, but some congregate with the males.

Most adults are long-lived. In cold climates some over-winter in sheltered places and in the dry tropics some aestivate through the dry season. Some undertake long dispersal flights, including transoceanic journeys, but others remain tightly associated with their larval habitat.

Mating: Odonate mating is an elaborate process. The male clasps the female by the head (Anisoptera) or prothorax (Zygoptera). The pair then fly together in tandem (male in front, female behind), often to a perch. The female bends her abdomen forward and downward to form the "wheel" position and connect with the secondary genitalia on segments 2-3 of the male, which previously have been charged with sperm from the primary genital opening on segment 9. Complex sperm displacement and sperm transfer activities then occur. A mating may last from several seconds to several hours, according to species.

In some species the pair lay eggs together, maintaining the tandem hold. In others the male hovers above the female while she lays her eggs. In some the male returns to his territory or perch while the female oviposits alone.



Xanthocnemis zealandica ovipositing (New Zealand)

Eggs are laid into plant tissues on, above, or below the water surface, or, in species without a functional ovipositor, are deposited onto the water surface or inserted into sand or mud. Egg development mostly is direct (ie, without diapause) and eggs takefrom 7-9 days to several months to hatch, according to species. Egg-stage overwintering is common in temperate climates. The egg hatches as a "prolarva" or 1st instar (actually a pharate 2nd instar) which wriggles to water if not already in it and then immediately undergoes ecdysis to the 2nd instar (first feeding, first free-living) stage.

Discussion of Phylogenetic Relationships

Higher Relationships

The relationships of Odonatoidea (= Odonata plus Protodonata) to the other pterygote insects continues to be much debated. For an outline see the attached note on Pterygote higher relationships.

Subordinal relationships in Odonata

Within the order Odonata, debate rages on several fronts. Which suborders are monophyletic and which are paraphyletic? Which fossil groups are "ancestral to" or closely related to which modern suborders? Is Zygoptera a paraphyletic basal grade from which Anisozygoptera and Anisoptera arose or are Zygoptera and Anisoptera each monophyletic groups, and is each derived from within suborder Anisozygoptera? There appears to be general agreement only that

- Odonata is a monophyletic group which has been separated from Ephemeroptera, Neoptera, and the extinct Palaeodictyopteroidea since at least the lowermost Upper Carboniferous
- The three extant suborders are closely related
- Fossil suborder Archizygoptera is a subset of fossil suborder Protozygoptera
- Modern Anisoptera is monophyletic

Wing venation

Hypotheses of the major phylogenetic relationships within Odonata depend critically on interpretation of the wing venation. Different schemes of wing vein homology across the suborders and alternative hypotheses of character-state transformation or polarity lead directly to different evolutionary hypotheses. Despite many efforts, consensus remains elusive. Attached is a brief note about differing views on Odonate wing venation.

Subordinal relationships

Consistent with their various conclusions on the evolution of the wing, different authors have proposed different subordinal phylogenies.

Handlirsch (1906-08) regarded Anisozygoptera as a "stem group" from which Anisoptera and Zygoptera arose as separate lineages. Tillyard (1928) regarded Zygoptera as basal, with Anisozygoptera derived from within Zygoptera and Anisoptera derived from within Anisozygoptera. Tillyard and Fraser (1938-40) treated Zygoptera and Anisozygoptera + Anisoptera as non-sister monophyletic groups, the former derived from Protozygoptera and the latter from Protanisoptera, but Fraser (1957) reverted to the Tillyard (1928) arrangement.

Hennig (1981) made Zygoptera the monophyletic sister group to Anisozygoptera + Anisoptera. He placed Anisozygoptera sister to Anisoptera. Carle (1982) followed Handlirsch (1906-08) in treating Anisozygoptera as basal but regarded both Zygoptera and Anisoptera as monophyletic. Carle and Wighton (1990) derived a polyphyletic Zygoptera by convergent reduction in the wing veins from anisopteran ancestors.

Trueman (1996) applied cladistic parsimony analysis to a set of wing vein morphological characters, finding in favor of Fraser's (1957) "paraphyletic Zygoptera, paraphyletic Anisozygoptera" hypothesis. In contrast, Bechly (1995, 1998), using a non-quantitative approach (Hennig's argumentation scheme) that assumes prior knowledge of ancestral character states and involves ad-hoc resolution of character conflict, favored a monophyletic Protozygoptera that is sister to the modern suborders, a paraphyletic Anisozygoptera, a monophyletic Zygoptera and monophyletic Anisoptera. Nel et al. (1993) and Lohmann (1996) made similar assumptions to Bechly and came to roughly similar conclusions.

Misof et al (2001) estimated the relationships of Anisoptera based on molecular sequence data, an approach that holds great promise for resolving the major, longstanding questions in odonate phylogeny. Their results differed significantly from those of Bechly (1998). Unfortunately, the terminal branches on their gene tree were in general long while internal branches were exceedingly short, a situation that makes the resolution of phylogenetic relationships exceedingly difficult. Misof et al. succeeded in recovering the majority of recognised family groupings in Anisoptera but had limited success with the inter-family relationships. On the basis of current fragmentary reports of data from other genes and other odonate taxa it seems likely that this hard-to-resolve pattern of long and short branches with marked non-stationarity in key parameters will hold across the whole order.

Rehn (2003) has produced a synoptic overview of odonate phylogeny that deserves to be considered in some detail. Rehn's scheme produces patterns with much appeal in both the Zygoptera (considered monophyletic) and in the Anisoptera + Epiophlebia (termed the 'Epiprocta'). The monophyly of the Zygoptera is supported by six characters, the two most important being the transverse head structure and the widely separated eyes, considered as derived characters. We are as yet unconvinced of the character polarity assumed here.

Kjer (2004) used the 18S sequence to evaluate relations in the Insecta. While generally very satisfactory, within the Odonata this study led to a rather unusual tree, with *Epiophlebia* at the base, the Anisoptera as a transition series, and with the Zygoptera as sister to a branch of the Libellulidae. Kjer comments on the credibility of the general tree produced and on the peculiar difficulties with the 'structure' within the Odonata.

Thus, at the present time, the jury remains firmly out. Even so, convergence toward one of two rival phylogenies can be discerned. The pattern of subordinal relationships would appear to be either as Tillyard (1928) and Fraser (1957) have it:

```
     ============================= Protodonata
     |
     |  ========================== Protanisoptera
=====|  |
     |  |  ======================= Protozygoptera
     ===|  |
        ===|          ============ Zygoptera (Coenagrionoidea)
           |          |
           =Zygoptera=|  ========= Zygoptera (Lestoidea, Calopterygoidea)
                      |  |
                      ===|  ====== Anisozygoptera (eg, Epiophlebia)
                         ===|
                            |  === Anisozygoptera (eg, Heterophlebia)
                            ===|
                               === Anisoptera
```

or else something along the lines first proposed by Handlirsch (1906-08). Using conventional names this may be represented as:

```
     ================================== Protodonata
     |
     |  =============================== Protanisoptera
=====|  |
     |  |  ============================ Protozygoptera
     ===|  |
        ===|                  |======== Zygoptera
           |                  |
           ==Anisozygoptera===|  ====== Anisozygoptera (eg, Epiophlebia)
                              |  |
                              ===|  === Anisozygoptera (eg, Heterophlebia)
                                 ===|
```

```
=== Anisoptera
```

. . . although within each broad class of phylogenies both the number and the ordering of branches within Zygoptera and Anisozygoptera are much disputed.

Classification

The established and widely accepted classification of extant families is as follows:

Zygoptera

- Hemiphlebioidea
  - Hemiphlebiidae
- Coenagrionoidea
  - Coenagrionidae
  - Isostictidae
  - Platycnemididae
  - Platystictidae
  - Protoneuridae
  - Pseudostigmatidae
- Lestoidea
  - Lestidae
  - Lestoideidae
  - Megapodagrionidae
  - Perilestidae
  - Pseudolestidae
  - Synlestidae
- Calopterygoidea
  - Amphyipterygidae
  - Calopterygidae
  - Chlorocyphidae
  - Dicteriastidae
  - Euphaeidae
  - Polythoridae

Anisozygoptera

- Epiophlebiidae

Anisoptera

- Aeshnoidea
  - Aeshnidae
  - Gomphidae
  - Neopetaliidae
  - Petaluridae
- Cordulegastroidea
  - Cordulegastridae

- Libelluloidea
  - Corduliidae
  - Libellulidae

(Classification from Watson and O'Farrell, 1991)

Alternative classification schemes have been recently proposed which erect many new taxonomic divisions and coin new names for old categories. To maintain stability we recommend use of the established and generally accepted classification until such time as the superiority of one or another of the newly proposed forms can be clearly established.

A listing of accepted extant species and of synonyms, maintained by Martin Schorr, Martin Lindeboom, and Dennis Paulson, is hosted at the University of Puget Sound. The family structure used in this listing varies slightly from that advocated above.

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Information on the Internet

A growing number of organizations and dragonfly enthusiasts maintain websites about dragonflies. Substantial and notable sites, as of October, 2001, include the following:

International Organizations:

- WDA Worldwide Dragonfly Association. Publishers of the journal INTERNATIONAL JOURNAL OF ODONATOLOGY.
- FSIO Foundation SIO. Publishers of the journal ODONATOLOGICA.

Regional Organisations:

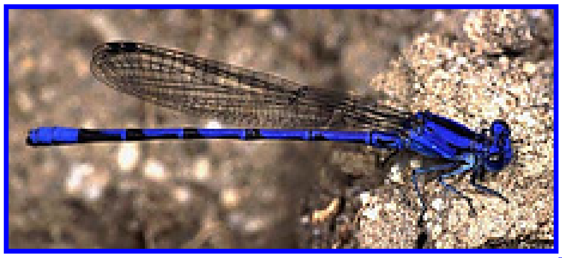
- IORI The International Odonata Research Institute. This organization, based in Florida, USA, is a good source of general information on Odonata and maintains extensive links to other dragonfly web pages.
- DSA The Dragonfly Society of the Americas brings together dragonfly workers and enthusiasts in North and South America.

Other notable Odonata pages:

- Takashi Aoki (Japan)
- Roy Beckemeyer (Kansas, USA)

- Martin Peterson (Sweden)
- Gordon Ramel (UK)
- Richard Rowe (Australia)
- Bishop Museum - Hawaii (Dan Polhemus)
- Slater Museum - Univ. of Puget Sound (USA) (Dennis Paulson)
- Digital Dragonflies A page with some high-quality images of Odonata.
- Phylogeny (Gunter Bechly) One view of odonate systematics.
- Odonata Links on the World Wide Web. Oregon Dragonfly and Damselfly Survey.

Title Illustrations



Scientific Name	Argia
Location	North America
Comments	Coenagrionid damselfly
Copyright	© 1997 Joseph L. Spencer

About This Page

Special thanks to Takashi Aoki for permission to use the image of Epiophlebia superstes, and to Larry J. Friesen, Peter Marsack, Stephen Richards and Joseph L. Spencer for other images.

This page compiled by:

John W. H. Trueman
John.Trueman@anu.edu.au
School of Botany and Zoology, Australian National University, Canberra, ACT 0200, AUSTRALIA

Richard J. Rowe
Richard.Rowe@jcu.edu.au
Department of Zoology & Tropical Ecology, School of Tropical Biology, James Cook University of North Queensland, Townsville, QLD 4811, AUSTRALIA

Correspondence regarding this page should be directed to John W. H. Trueman at John.Trueman@anu.edu.au

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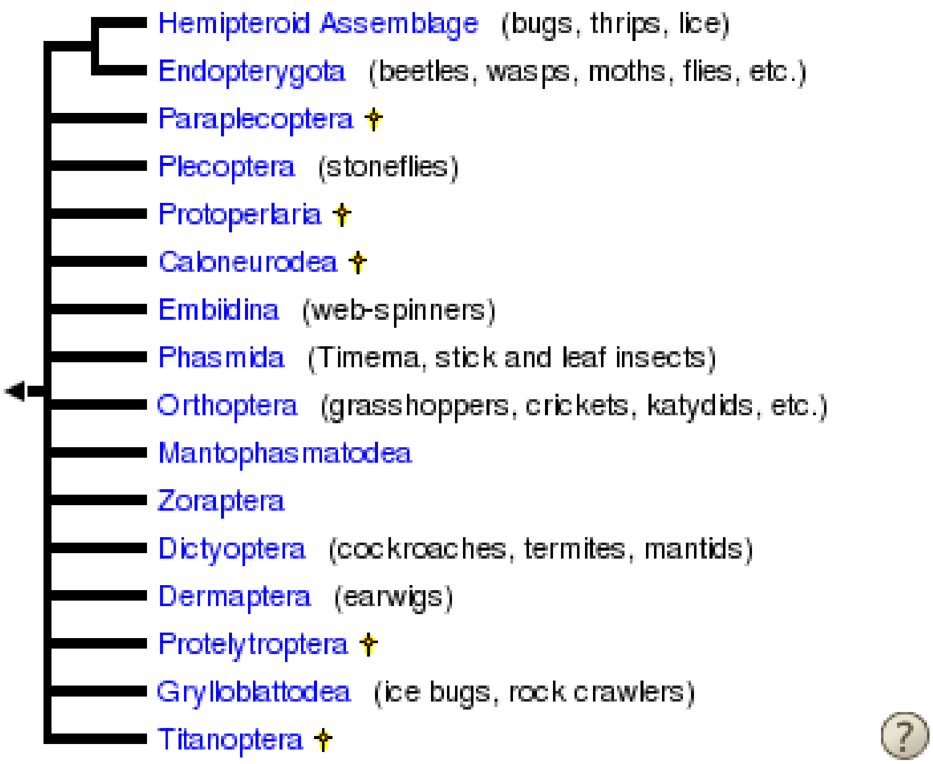
Neoptera



Containing group: Pterygota

Introduction

The neopterous insects include the Hemipteroid Assemblage, Endopterygota, as well as the "lower Neoptera". The "lower Neoptera" include the Plecoptera, Embidiina, Zoraptera, and the "orthopteroid" orders (all the remaining living orders shown in the tree above).

Characteristics

Neopterous insects primitively have the ability to fold the wings back over their abdomen, using special structures at the base of their wings. Key to the folding mechanism is the third axillary sclerite and pleural wing-folding muscle.

This ability to fold the wings back over the abdomen has been lost in some small groups within Neoptera, including various butterflies and moths.

Discussion of Phylogenetic Relationships

The relationships of the orthopteroid orders to one another, and their relationship to plecopterans (stoneflies), embiids (web-spinners), and zorapterans, are unsettled. The placement of the plecopterans, embiids, and zorapterans are perhaps the most enigmatic.

Hennig (1969, 1981) considered the zorapterans to be sister to the hemipteroid complex, the stoneflies to be relatively basal, and the web-spinners to be the sister group to the orthopteroid orders:

```
              ========= Hemipteroid Assemblage
           ===|
     ======|  ========= Zoraptera
     |     |
     |     ============ Endopterygota
     |
     |================= Plecoptera
     |
     |     ============ Embiidina
=====|     |
     |     |     ====== Orthoptera
     |     |  ===|
     |     |  |  ====== Phasmida
     ======|  |
           ===|  ====== Grylloblattodea
              |  |
              ===|  === Dermaptera
                 ===|
```

```
                    === Dictyoptera
```

Boudreaux (1979) considered the web-spinners to be the sister to stoneflies with zorapterans nested within the orthopteroids:

```
           ============ Hemipteroid Assemblage
     ======|
     |     ============ Endopterygota
     |
     |     ============ Plecoptera
     |=====|
     |     ============ Embiidina
     |
     |        ========= Orthoptera
=====|     ===|
     |     |  ========= Phasmida
     |     |
     |     |  ========= Dermaptera
     ======|  |
           |  |  ====== Grylloblattodea
           ===|  |
              ===|  === Zoraptera
                 ===|
                    === Dictyoptera
```

More recent analyses using molecular data have still not been able to establish a well supported hypothesis of neopteran relationships; e.g., Flook and Rowell (1998) suggested the following topology based on their analysis of SSU rRNA sequences (Endopterygota and Zoraptera not included in analysis):

```
     =============== Hemipteroid Assemblage
     |
     |  ============ Dictyoptera
=====|  |
     |  |     ====== Grylloblattodea
     |  |     |
     |  |=====|===== Plecoptera
     ===|     |
        |     ====== Dermaptera
        |
        |        === Phasmida
        |     ===|
        ======|  === Embiidina
```

```
              |
              ====== Orthoptera
```

Wheeler et al. (2001) favor the following relationships based on a combined analysis of morphological and molecular data:

```
        ========= Hemipteroid Assemblage
     ===|
     |  ========= Endopterygota
     |
     |     ====== Zoraptera
     |     |
=====|     |===== Dictyoptera
     |  ===|
     |  |  |===== Dermaptera
     |  |  |
     |  |  ====== Grylloblattodea
     ===|
        |     === Phasmida
        |  ===|
        |  |  === Orthoptera
        ===|
           |  === Embiidina
           ===|
              === Plecoptera
```

The tree shown at the top of this page reflects the cautious views of Kristensen (1991), and is perhaps a clearer indication of our current knowledge about relationships of these orders.

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Title Illustrations

Scientific Name	Dactylotum variegatum
Comments	A grasshopper (Orthoptera)
Specimen Condition	Live Specimen
Copyright	© 1995 Joseph L. Spencer

Scientific Name	Halictidae
Comments	A halictid bee (Endopterygota: Hymenoptera)
Specimen Condition	Live Specimen
Copyright	© 1995 Joseph L. Spencer

Scientific Name	Pyrrhocoris apterus
Comments	A bug (Hemipteroid Assemblage)
Creator	Photograph by Jean-François Cornuet
Specimen Condition	Live Specimen
Copyright	© BIODIDAC

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Dermaptera

Earwigs

Fabian Haas

- Archidermaptera ✝ (non-monophyletic)
- Hemimerina
- Arixenina
- Forficulina

Containing group: Neoptera

Introduction

Earwigs or Dermaptera constitute a comparatively small order of insects comprising about 1800 species. Their scientific name refers to the leathery fore wing (dermatos: skin, pteron: wing, both words of Greek origin) and was given by de Geer in 1773. However, he used the name for all orthopteroids. It was Kirby in 1815 who introduced the name in the modern sense.

Dermaptera are elongate and slender insects with a prognathous head. If not wingless, the thorax bears two pairs of wings of which the first one is small and leathery, called tegmina. The second pair is large and membraneous (see fig. below), almost semi-circular, and, at rest, folded underneath the tegmina in a complicated manner. The abdomen of extant Dermaptera is highly movable with a pair of unsegmented (not always forceps-like) cerci at its posterior end. The body length ranges from approximately 4 to 80 mm including cerci. Most Dermaptera are uniformly coloured brown or black, sometimes with a light brown or yellow pattern; other colours, like metallic green are real exceptions. They are distributed throughout the world (except the polar regions), with greatest diversity in the tropics.

Not very much is known about the natural history of the Dermaptera as a whole, with the species studied in some detail being mostly European. So "the earwig" is Forficula auricularia, the common earwig; other well studied species are Labidura riparia, the striped earwig and Anisolabis maritima, the seaside earwig.

Most species are omnivorous but predominantly phytophagous or predacious species are also known. Some species live on decaying material. The Hemimerina feed on scurf and fungi on the skin of giant rats without harming them. The Arixenina feed on skin gland secretions of bats and occasionally on dead insects.

Dermaptera are thigmotactic (searching close contact to surfaces). They frequent (humid) crevices of all kinds: you can find them under bark, between leaves and under stones. Probably, earwigs also creep in human ears just taking them for humid and warm crevices to hide. This behaviour probably gave rise to the belief that they penetrate the tympanum and lay eggs in the brain, which is utter nonsense. Therefore their name in colloquial speech often refers to the ear, like in Danish, Dutch, English, French, German, Russian and Swedish, or to the forceps, like Italian, Finnish, Portuguese and Spanish. The behaviour of Dermaptera is complex and the cerci seem to play an important role. They are used to open the wings, to capture prey and for defence. Females show maternal care.

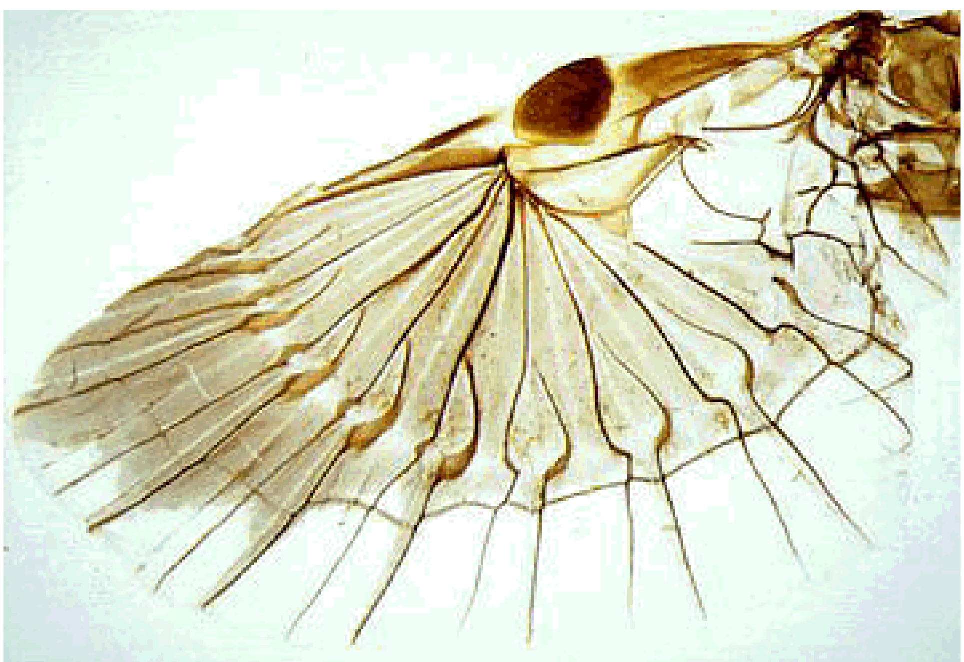
The development is hemimetabolous. The larvae (4 to 5 instars) resemble the adult apart from having only wing buds. However, in wingless species the larvae are often difficult to distinguish from the adults. The larva's cerci are simple, almost straight and resemble those of the female. Vivipary occurs in all Hemimerina and Arixenina but is not known from the Forficulina, which are generally oviparous.

The fossil record of the Dermaptera begins in the Jurassic (Carpenter, 1992), about 208 million years ago and comprises about 70 specimens. The earliest fossils are very similar to Recent species but adults have segmented cerci. No fossil Hemimerina and Arixenina are known. The probable stem group of the Dermaptera are the Protelytroptera (Carpenter, 1992; Hennig, 1969). These insects, which resemble modern Blattodea or Cockroaches, are known from the Permian (about 290 MYA) of North America, Europe and Australia (Carpenter, 1992). There are no fossils from the Triassic when the morphological changes from Protelytroptera to Dermaptera took place.

The Dermaptera are often considered a neglected group. However, there are a number of monographs and regional faunas with a large general section, which give a good introduction to their biology: Albouy & Caussanel (1990), Beier (1953, 1959), Bey-Bienko (1936), Bormans & Krauss, (1900), Brindle (1972), Burr (1910), Carpenter (1992), Chopard (1938, 1949), Günther & Herter (1974), Harz (1960), Rentz & Kevan (1991), Sakai (1970-1996), Steinmann (1986, 1989, 1990, 1993).

Characteristics

Even though Dermaptera are easily recognized, it is not easy to find synapomorphic characters for the whole order. Most striking are unsegmented, forceps-like cerci, however, they are not forceps-like in the Hemimerina and Arixenina. Furthermore, unsegmented cerci occur in many orthopteroids.



Unfolded wing of Allodahlia scabriscula, Forficulina: Forficulidae

The morphology of their tegmina and hind-wings could constitute a synapomorphy but the Hemimerina and Arixenina are wingless. Maternal care is remarkable but only a few species have been studied. However, the occurence of maternal care in the very primitive genus Diplatys and in the highly derived genus Forficula suggests that this is a common trait for all Forficulina. There are almost no observations concerning maternal care in Hemimerina and Arixenina. In female Forficulina and Hemimerina, the tergites of abdominal segment 8 and 9 are narrow, fused and covered by the tergite of segment 7. However, this is not true for the Arixenina (Giles, 1963). The tarsi have three segments in all Recent suborders. In all Dermaptera, the first abdominal sternite is lacking and the tergites and sternites are overlapping laterally. A cytological trait, holocentric chromosomes, probably is the most convincing synapomorphy. It is found in all Recent suborders and is unique in orthopteroid insects (Rentz & Kevan, 1991).

The Suborders of Dermaptera

The Dermaptera are divided into four suborders.

The Archidermaptera comprise ten fossil species from the Jurassic with segmented cerci in adults and four or five segmented tarsi (Bey-Bienko, 1936). Both character states are considered primitive for Dermaptera and used as diagnostic features.

The Forficulina are by far the largest group comprising about 1800 species in 180 genera, including the common earwig and the striped earwig. The body shape of these species is characteristic for the whole suborder. The species are omnivorous, phytophagous or predacious. The adult cerci are unsegmented and forceps-like. The larval cerci are unsegmented except in two primitive groups. If not wingless, the hind wings are complexly folded in a unique way, and covered by tegmina.

The viviparous Hemimerina comprise ten species in one genus living epizoically on giant rats in tropical Africa. They are wingless, blind, about 10 mm long excluding the filiform cerci, and possess short and stout legs. Their body is streamlined and smooth for rapid movement through the fur.

The viviparous Arixenina comprise five species in two genera and live on bats in the Malayan-Philippinian region. They are wingless, almost blind, possess straight rod-like cerci and have long and slender legs.

Discussion of Phylogenetic Relationships

The phylogenetic relationships of the four suborders are not well understood. The suborders are usually described separately because they are cleary different in morphology and natural history. The discussion of their relationships have been further complicated because no phylogenetic system has been available for the Forficulina. Therefore, the evolution of characters remained obscure, which otherwise could help to interpret the characters of the highly derived Hemimerina and Arixenina. The discussion of their relationships was largely based on considerations of similarities and differences between the groups and not on a cladistic analysis of characters.

The systematic position of Hemimerus was subject to considerable change in the first years after its discovery. It is beyond the scope of this page to give a detailed account of the discussion but the topic was whether or not Hemimerus should be placed in a separate order or included in the Dermaptera (for a detailed account see Giles (1963)). The subordinal rank was given by Burr (1911). The genus Arixenia was first described by Jordan (1909). Again, Burr (1911) erected a new suborder, the Arixenina. So, the widely accepted view (for example Sakai (1982)) that the order Dermaptera consists of three Recent suborders is based on Burr (1911).

In 1985, Popham re-assessed the relationships of the Dermapteran suborders and families using cladistic methods. His phylogenetic system is mainly based on characters of the genitalia:

```
  === Hemimerina
  |
  |  === Pygidicranidae
==|  |
  |  |     === Carcinophoridae (Anisolabididae)
  ===|     |
     |  ===|  === Arixeniidae
     |  |  ===|
     ===|     === Labiidae (Spongiphoridae)
        |
        |     === Labiduridae
        |     |
        ======|  === Chelisochidae
              ===|
                 === Forficulidae
```

The Hemimerina are still regarded as a suborder, whereas the Arixenina are treated as the probable sistergroup of Spongiphoridae, accordingly called Arixeniidae. Popham's view has not been generally accepted. He split traditional groups, like the Eudermaptera

(Spongiphoridae+Chelisochidae+Forficulidae) and regarded the Carcinophoridae to be wingless. However, there is a fair number of fully winged species in this family, among them Carcinophora americana. Other characters have been criticized by Haas (1995), Willmann (1990) and Günther & Herter (1974) referring to Popham (1965). Steinmann (1986) regards Dermaptera to consist of only Forficulina. However, this view is not widely shared.

The position of the extinct Archidermaptera has hardly been discussed. Unsegmented adult cerci and four or five segmented tarsi are generally regarded as plesiomorphic character states. Willmann (1990) presented the first phylogenetic study. He concluded that the Archidermaptera should be regarded as sistergroup of the remaining suborders.

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Title Illustrations

Scientific Name	Hemimerus talpoides
Comments	Hemimerina
View	lateral view
Copyright	© 1996 Fabian Haas

Scientific Name	Arixenia esau
Comments	Arixenina
Copyright	© 1996 Fabian Haas

Scientific Name	Forficula auricularia
Comments	Forficulina: Forficulidae
Copyright	© 1996 Fabian Haas

About This Page

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Fabian Haas
mailto:webmaster@earwigs-online.de
Institut f?r Spezielle Zoologie und Evolutionsbiologie
Erbertstr. 1
D-07743 Jena
Germany

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Dictyoptera

Isoptera (termites)
Mantodea (mantids)
Blattaria (cockroaches)

Containing group: Neoptera

Discussion of Phylogenetic Relationships

Boudreaux (1979), Thorne & Carpenter (1992), DeSalle et al. (1992), Kambhampati (1995), and Wheeler et al. (2001) argue for a sister group relationship between mantids and cockroaches:

```
     ====== Isoptera  (termites)
  ===|
     |  === Mantodea  (mantids)
     ===|
        === Blattaria  (cockroaches)
```

Hennig (1981), Kristensen (1995), Klass (1998), and Lo et al. (2000) favor a sister group relationship between termites and cockroaches:

```
     ====== Mantodea  (mantids)
  ===|
     |  === Isoptera  (termites)
     ===|
```

=== Blattaria (cockroaches)

The monophyly of cockroaches has often been questioned, and many authors believe that the Blattaria are paraphyletic with respect to the Isoptera. In particular, a sister group relationship between Isoptera and Cryptocercus wood roaches has often been suggested (e.g., McKittrick 1964, Hennig 1981, Lo et al. 2000).

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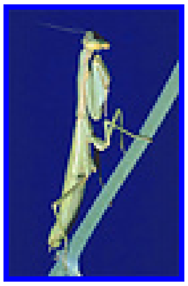
Title Illustrations



Scientific Name	Stagmomantis carolina (Mantodea)
Comments	Carolina mantis
Creator	Marguerite Gregory
Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
Copyright	© 1999 California Academy of Sciences

Scientific Name	Coptotermes formosanus (Isoptera)
Comments	Formosan subterranean termite
Acknowledgements	Courtesy InsectImages.org (#0014115)
Specimen Condition	Live Specimen
Life Cycle Stage	Worker
Copyright	© Gerald J. Lenhard

Scientific Name	Parcoblatta pennsylvanica (Blattaria)
Comments	Pennsylvania wood cockroach
Specimen Condition	Live Specimen
Sex	Male
Copyright	© Department of Entomology, University of Nebraska-Lincoln

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Correspondence regarding this page should be directed to David R. Maddison at

beetle@ag.arizona.edu

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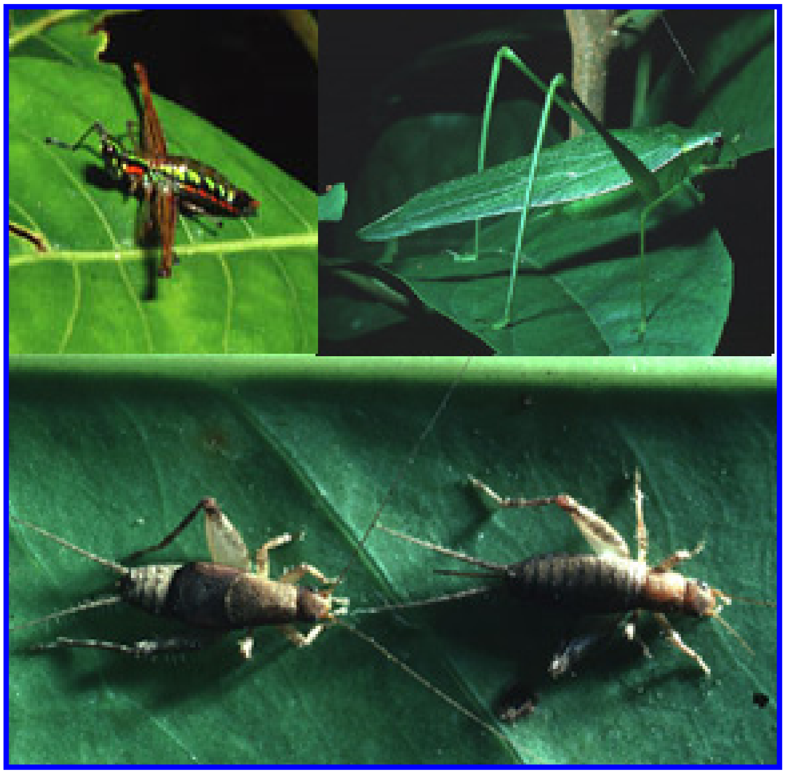
- Ensifera

Orthoptera

Crickets, katydids, grasshoppers, etc.

Darryl T. Gwynne, Laure DeSutter, Paul Flook, and Hugh Rowell



- Ensifera (Crickets, katydids and weta)
- Caelifera (Shorthorned grasshoppers and locusts)

Containing group: Neoptera

Introduction

The more than 20,000 species in this order have a worldwide distribution but are most diverse in the tropics. Body size varies from less than 5 mm to some of the world's largest insects, with body lengths up to 11.5 cm, and wingspans of over 22 cm. Orthopterans are a common component of terrestrial insect faunas and include some of the most voracious pests (locusts and certain katydids). Members of both suborders are generally phytophagous but many species are omnivores. Females of most species lay clutches of eggs, either in the ground or in vegetation. Some of the best examples of cryptic coloration are seen in this group, involving mimicry of leaves and other vegetation or other resemblance to the background (Chopard 1938; Hewitt 1979; Kevan 1982; Rentz 1991). Grasshoppers, katydids and crickets are well known for their abilities to jump and particularly for singing by males (females are typically silent). There are few places in the world where the calls of grasshoppers (usually diurnal), katydids and crickets (usually nocturnal) cannot be heard during warm seasons. Organs of sound production and sound reception involve quite different body parts in the two subgroups (Alexander 1960; Dumortier 1963).

The first fossil Orthoptera appear in the upper Carboniferous with the first Ensifera (Chopard 1920) appearing in the Permian and the first Caelifera (Ander 1939) in the Triassic (Gorochov 1995; Kukalova-Peck 1991; Sharov 1968; Zeuner 1939). The two groups are usually considered suborders of the Orthoptera. Attempts to create a separate order for the two suborders Caelifera and Ensifera (e.g. Kevan 1986, in which Ensifera = Grylloptera) have not found general entomological acceptance (see Discussion of Phylogenetic Relationships).

Characteristics

The name Orthoptera is derived from "orthos" meaning "straight" and "pteron" = "wing."

Shared-derived characters: in addition to the saltatory hind legs, most orthopterans have small and well separated hind coxae, a pronotum with large descending lateral lobes, nymphal wing rudiments reversing their orientation in later instars and hind tibiae with two dorsal teeth rows (Kevan 1982; Kukalova-Peck 1991; Rentz 1991). Other characteristics are unsegmented cerci and leathery forewings.

Discussion of Phylogenetic Relationships

General opinion favors a monophyly hypothesis for the order Orthoptera (Hennig 1981; Gorochov 1995). Most studies have examined extant taxa. Although numerical analyses of orthopteroid character distributions (mainly phenetic) by Blackith (1968) show the Blattodea-Mantodea clade and not Caelifera as the sister group of Ensifera, Kamp's (1973) analysis of a more expanded morphological character matrix supports monophyly. Kristensen's (1991) discussion also supports monophyly. Formal analyses of molecular characters (Flook and Rowell 1997) also support the conventional view of a unitary order Orthoptera. For discussions that include extinct taxa, Kukalova

Peck (1991) suggests the group may not be monophyletic but Gorokhov (1995) supports monophyly. A sister group relationship between Ensifera and Phasmatodea has been proposed (Sharov 1968), but this is inconclusively supported according to Kristensen (1995) who suggested that the characters involved (wing venation) are not synapomorphies. Molecular data show a unitary Orthoptera as the sister group of a clade comprising the Phasmida and the Embiidina (Flook and Rowell 1998, Flook et al. 1999). Trees of extinct and extant Orthoptera (Sharov 1968; Zeuner 1939) show Caelifera as derived from a primitive ensiferan stock (not more recently than the Permo - Triassic boundary). However both authors show all extant groups as monophyletic. This interpretation is consistent with the numerical analyses of morphological characters in orthopteroid insects (Blackith and Blackith 1968; Kamp 1973), a recent review of the phylogeny of extant hexapods (Kristensen 1991), and molecular sequence data (Flook and Rowell 1998, 1999, non-technically reviewed by Rowell and Flook 1998).

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Information on the Internet

- Orthopterist's society homepage

- Orthoptera del Noreste amazónico
- The Orthoptera Species File Online (a taxonomic database of the world's orthopteroid insects)

Title Illustrations

Scientific Name	Orthoptera
Location	Columbia
Comments	Top: Columbian acridid (left) and tettigoniid (right) (photos by Dita Klimas). Bottom: mogoplistids (Ornebius aperta) (D.T. Gwynne)
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About This Page

Darryl T. Gwynne
dgwynne@credit.erin.utoronto.ca
Zoology Department, Erindale Campus, University of Toronto, Mississauga, Ontario Canada L5L 1C6

Laure DeSutter
desutter@cimrs1.mnhn.fr
Entomologie, Museum National d'Histoire naturelle, 45 rue Buffon, F - 75005, Paris, France

Paul Flook
paul.flook@gcg.com
Genetics Computer Group, 575 Science Drive, Madison, WI 53711, USA

Hugh Rowell
hrowell@datacomm.ch
Zoology Institute, University of Basel, Rheinsprung 9, Basel 4051, Switzerland

Correspondence regarding this page should be directed to Darryl T. Gwynne at dgwynne@credit.erin.utoronto.ca

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Ensifera

Crickets, katydids and weta

Darryl T. Gwynne and Laure DeSutter

Ensifera tree modified from Gwynne (1995).
Containing group: Orthoptera

Introduction

Ensiferans are the "longhorned" orthopterans identified by their characteristic threadlike antennae which can reach to several times the body length. The group is largely nocturnal and many taxa are long-lived with adult life spans of over a year. Females inject eggs into plant material or soil through a long ovipositor (Chopard 1938, Beier 1972, Kevan 1989, Rentz 1996). Several taxa that have a reduced or absent ovipositor show maternal care of eggs or nymphs (Gwynne 1995). Ensiferans include most of the major groups of singing insects, taxa in which males stridulate to call mates. Stridulation involves rubbing together modified portions of the forewings in katydids (or bush-crickets (Tettigoniidae)) (Bailey and Rentz 1990), true crickets and their allies (Otte 1992, Desutter 1995) and Haglidae (Morris and Gwynne 1978) and a femur-abdominal mechanism in certain weta (Stenopelmatidae) (Field 1993). The more than 9000 described species in the suborder show a broad range of habits and habitats . They are found worldwide in diverse habitats. Some species retreat to crevices and burrows (Kevan 1989), an ancestral habit (Gwynne 1995) whereas others avoid natural enemies with a remarkable mimicry of leaves and other plant parts.

The six families in the tettigonioid clade range in diversity from only a few species in groups such as the relict Haglidae, the hump winged and ambidextrous crickets, to the 6000 or so katydids (bush-crickets) (Tettigoniidae) (Beier 1955; Otte, 1997). Other tettigonioids are: Stenopelmatidae which includes New Zealand's giant weta (among the world's heaviest insects), tree weta and ground weta (Gibbs 1994) as well as Jerusalem crickets and king crickets (Rentz 1996); Cooloolidae, a completely subterranean family from north eastern Australia (cooloola monsters) (Rentz 1996); Gryllacrididae, the raspy and leaf rolling crickets; and Rhaphidophoridae, the camel and cave crickets and cave weta. The remaining ensiferan taxa are splay-footed crickets (Schizodactylidae) of India and Africa, and the 3000 or so species of "true" crickets (including house, field, ground, tree and bush crickets) (Otte 1994).

Zeuner (1939), Sharov (1968) and Gorochov (1995a,b) review the fossil history of Ensifera. The first fossils are from later Carboniferous. Sharov (1968) lists a number of extinct families and represents Ensifera as a paraphyletic taxon (showing the order Phasmatodea and suborder Caelifera as being derived from ancestral ensiferan stock) but places all extant families in one clade. Gorochov (1995a) recognizes two extinct ensiferan infraorders, Elcanidea and Oedischiidea, placing all extant (and some extinct) taxa in the infraorders Tettigoniidea and Gryllidea. Not included in the four groups are the extinct Phasmomimoidea and Vitimiidae, the relationships of which are unclear.

Figure 1. A third ensiferan family, Stenopelmatidae: a Jerusalem cricket (Stenopelmatus fuscus)

Characteristics

The antennae are fine and threadlike (well over 30 segments) except in the completely fossorial Cooloolidae. In the singing families there are stridulatory specializations of the forewings which include a toothed vein (file) and scraper, and membranous areas that resonate or amplify sounds. In these groups ears consist of foretibial tympanae linked via modified tracheae to the enlarged mesothoracic spiracles that are modified for an auditory function. The tarsi have three to four segments. The six-valved ovipositor (when present) is sword-like ('ensiform', thus the subordinal name) or needle-like (Chopard 1920; Kevan 1982; Rentz 1991, 1996). Ensiferan mandibles are elongate and possess a prominent incisor. The gut's proventriculus consists of a globular body lying between two bulbous gastric caeca. Internally there are six longitudinal folds that bear appendages (Judd 1947; Rentz 1980). The spermatophore in virtually all species is attached externally to the female's gonopore; it has a double (or partially divided) sperm reservoir in most Tettigonioidea (some Rhaphidophoridae and Deinacrida species (Stenopelmatidae) are exceptions) and a single one in true crickets and their allies. In many taxa (most tettigonioids and some true crickets) a spermatophylax (meal for the female) surrounds the spermatophore (Boldyrev 1915; Gwynne 1995).

Classification

A number of different classification schemes have been proposed. Chopard's (1938) Orthoptera book listed the families Tettigoniidae, Prophalangopsidae (= Haglidae), Gryllacrididae and Gryllidae. Zeuner's (1939) study of Ensifera increased the list by separating Gryllotalpidae from Gryllidae, and Ander (1939) by elevating several subfamilies of Gryllacrididae to family level: Stenopelmatidae, Schizodactylidae and Rhaphidophoridae (Sharov (1968) again reduced the last family to subfamily level). A few schemes (Chopard 1949, Kevan 1982, Gorochov 1995b) propose many more families (raising many subfamilies to family rank and certain families to superfamily rank). For stability and the fact that such changes add little to understanding inter-relationships (Ragge 1977) this page follows the conventional group names (of Ander) used in most of the recent Orthoptera classification schemes (Judd 1949, Beier 1972, Key 1970, Ragge 1977, Rentz 1991, Otte 1997). The only changes are the addition of the recently discovered family Cooloolidae (Rentz 1980) and grouping together the Gryllidae and Gryllotalpidae (and related taxa) as "true crickets and their allies" form a separate clade (see Desutter 1987). Two ensiferan families referred to in previous work, Lezinidae and Henicidae, are subgroups of the Stenopelmatidae (but see the Discussion of Phylogenetic Relationships, below). Dolichopodidae is a subgroup of Rhaphidophoridae

Most authors divide ensiferan families into two to four higher taxa (infraorders (Kevan 1982, Gorochov 1995a) or superfamilies (Ander 1939, Zeuner 1939, Judd 1947, Key 1970, Ragge 1977, Rentz 1991)). The three superfamilies of Beier (1972), Key (1970) and Rentz (1991) (Tettigonioidea, Gryllacridoidea and Grylloidea) are shown as separate clades only in the trees of Zeuner (1939) and Ragge (1955). Here we follow Ander (1939), Judd (1949), Ragge (1977) and Gwynne (1995) and use a two-fold division of the Ensifera, recognizing the two distinct clades (see also Ragge 1977).

Discussion of Phylogenetic Relationships

Monophyly of terminal taxa. No formal analysis of characters has been done for any group except Desutter's (1987) treatment of neotropical taxa of true crickets and allies which shows these taxa to form a clade. The characters of the other most diverse taxon, Tettigoniidae, suggests that it is monophyletic (Hennig 1981), a conclusion supported by Gorochov's (1995b) tree. Gryllacridid and rhaphidophorid characters also suggest monophyly for these families (Rentz pers. comm. and Cohn, pers comm.). Gorochov (1995b) depicts the subgroups (both extinct and extant) of both the rhaphidophorids and haglids as forming separate clades. No author has suggested that the least diverse families, Cooloolidae (one genus) and Schizodactylidae (two genera) are not natural groups. Stenopelmatidae is, however, problematical. P. Johns (submitted) suggests that the Gonwanaland weta and related taxa (mainly antipodean) should be placed in a separate family (Anostostomatidae) from the Jerusalem crickets and allies (Stenopelmatidae). A similar scheme (but using Mimnermidae instead of Anostostomatidae) was suggested by Gorochov (1995b).

There is no consensus on the evolutionary history of the relationships among families. The cladogram of extant groups suggested by Gwynne (1995) (see above) is a hypothesis based on a formal analysis of (morphological) characters. The single most parsimonious cladogram is identical to Ander's (1939) tree (a detailed and thorough review of ensiferan morphological characters) except for the position of Schizodactylidae, which Ander placed in the Tettigonioidea. In Gwynne (1995) this family is weakly placed as a sister group to true crickets and allies (less than 50% of bootstrap replications). The relationship of Schizodactylidae with other Ensifera has always been unclear (see Ander (1939)); schizodacylids have even been given equal taxonomic ranking to the other main Ensifera subgroups by some authors (e.g. Kevan 1982).

Sharov's (1968) tree of extinct and extant Ensifera is often cited. His interpretation, based on the stridulatory organ and other wing characters, is unique in the closer relationship between the singing families Haglidae and the true crickets and allies rather than with the tettigoniids (see figure). Hennig (1981) and Kevan (1977) are critical of this tree and a more recent treatment of fossil and living ensiferans shows the more common conclusion for relationships among singing families i.e. a closer relationhip between Haglidae and Tettigoniidae (Gorochov 1995b).

```
              ========= Haglidae
              |
              |  ====== Rhaphidophoridae
           ===|  |
        ===|  ===|===== Stenopelmatidae
     ===|  |     |
=====|  |  |     ====== Gryllacrididae
     |  |  |
     |  |  ============ Schizodactylidae
     |  |
     |  =============== true crickets and allies
     |
     ================== Tettigoniidae
```

Sharov's (1968) tree of extant Ensifera (Sharov includes stenopelmatids and rhaphidophorids in one family, Gryllacrididae)

All other trees (Zeuner 1939; Ragge 1955; Gorochov 1995) show Tettigoniidae and Haglidae as sister taxa. These trees regard tegminal stridulation and tibial ears as homologous within Ensifera whereas the most parsimonious interpretation using Ander (1939) and Gwynne (1995) is a dual origin of these characters.

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Information on the Internet

- Orthopterist's society homepage
- The Katydids of La Selva (Costa Rica)
- University of Florida Natural Area & Teaching Lab: crickets & katydids.
- The Orthoptera Species File Online (a taxonomic database of the world's orthopteroid insects)
- Keys and species lists of North American crickets and katydids
- Crickets in Chinese Culture

Title Illustrations

Scientific Name	Cooraboorama canberrae
Comments	Gryllacrididae
Sex	Female
Copyright	© 1996 Darryl T. Gwynne

Scientific Name	Metholche nigritarsus (Conocephalinae)
Specimen Condition	Live Specimen
Sex	Male
Copyright	© Darryl T. Gwynne

About This Page

Thanks to Pat Lorch and David Rentz for comments.

Darryl T. Gwynne
dgwynne@credit.erin.utoronto.ca
Zoology Department, Erindale Campus, University of Toronto, Mississauga, Ontario Canada L5L 1C6

Laure DeSutter
desutter@cimrs1.mnhn.fr
Entomologie, Museum National d'Histoire naturelle, 45 rue Buffon, F - 75005, Paris, France

Correspondence regarding this page should be directed to Darryl T. Gwynne at
dgwynne@credit.erin.utoronto.ca

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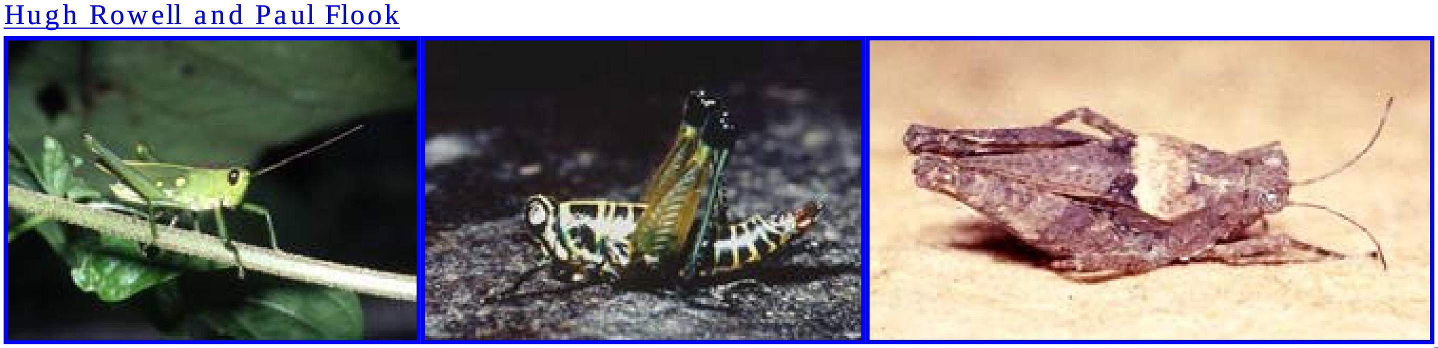
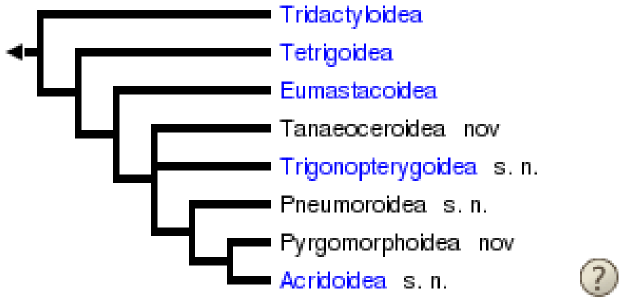
Caelifera

Shorthorned Grasshoppers, Locusts and Relatives

Hugh Rowell and Paul Flook





Phylogeny derived from ribosomal gene sequences (Flook and Rowell 1998, Flook et al. 2000).
Containing group: Orthoptera

Introduction

Recent estimates (Kevan 1982; Günther, 1980, 1992; Otte 1994-1995; subsequent literature) indicate some 2400 valid Caeliferan genera and about 11000 valid species described to date. Many undescribed species exist, especially in tropical wet forests. The Caelifera are predominantly tropical, but most of the superfamilies are represented world wide.

By insect standards the Caelifera are relatively homogenous; all have jumping back legs and are almost exclusively herbivorous. None the less they show considerable diversity. As adults they range in size from a few millimetres to more than 15 cm in length, are flighted or flightless, occupy virtually all non-marine habitats in which plants can live (including deserts, water surfaces, the crowns of forest trees, grasslands, or underground); they eat algae, mosses, the leaves and reproductive organs of ferns, gymnosperms and angiosperms, or even the roots of the latter, with all degrees of foodplant specialisation from wide-range polyphagy to strict monophagy.

The Caelifera are probably the oldest living group of chewing folivorous insects. The Tettigonioidea may predate them geologically, but it is unclear how herbivorous these were, as many Tettigonioids are even now still carnivorous or omnivorous. The fossil Caelifera are reviewed by Zeuner (1941-1944), Sharov (1971), Kukalova-Peck (1991), Carpenter (1992) and Ross & Jarzembowski (1993). The split between the Caelifera and the Ensifera is not more recent than the Permo-Triassic boundary (Zeuner 1939). The earliest known representatives of an extant Caeliferan Superfamily are the extinct *Regiatidae (Tridactyloidea) from the Lower Jurassic (Gorochov 1995). Essentially modern Eumastacids are known from the mid-Jurassic, modern Tridactyloids and Tetrigoids from the early Cretaceous, Acridoids from the Eocene. Most, possibly all, of the modern superfamilies probably developed in the Jurassic.

Characteristics

Among other synapomorphies the Caelifera is distinguished from the Ensifera by the structure of the ovipositor, in which the original 6 valves are reduced to 4 functional ones with transverse musculature, by antennae composed of less than 30 segments, and by the absence of auditory organs on the prothorax - if a tympanum or other hearing organ is present, it is abdominal. The sperm are thin and elongate, with an acrosome inserted on the nucleus by means of two lateral processes.

Discussion of Phylogenetic Relationships

A conservative view of caeliferan relationships is shown in **Figure 4**. Due to the virtual absence of explicit schemes in the modern literature, this hypothesis follows no particular publication, but it is shared by most modern morphologists (Rentz, 1991).

```
    ================= Tridactyloidea
```

```
 ===|
    |  =============== Tetrigoidea
   ===|
      |  ============ Eumastacoidea
     ===|
        |  ========= Trigonopterygoidea
       ===|
          |  ====== Pneumoroidea
         ===|
            |  === Pamphagoidea
           ===|
              === Acridoidea
```

Figure 4: Phylogeny based on morphology, modified after Dirsh (1975).

As in several of the insect orders, few formal phylogenetic analyses of the Caelifera have been undertaken. The major sources of phylogenetic opinion lie in the Discussion sections of primarily taxonomic or morphological publications, and are rarely supported by explicit data. Cladistic analysis of morphological data matrices is rare. Only recently have molecular data been used to examine phylogenetic relationships within this group.

One category of phylogenies is derived from wing venation, as exemplified by the schemes of Zeuner, Sharov, Ragge and Gorochov. In these works, however, the emphasis is on the Ensifera, which have a much more extensive fossil record, and the Caelifera are not treated in detail. Further, some of the Caeliferan relationships implicit in the scheme proposed by Sharov are not supported by any obvious evidence (see e.g. the critique in Amédégnato, 1993). A further problem lies in the identification of the plesiomorphic form of the venation. For example, Ragge concluded that the Pneumorids were the most primitive Caeliferans on the basis of the similarity of their venation with that of the Palaeozoic *Palaeodictyoptera. However, as these are not considered to be ancestral to the orthopteroid insects, their significance in this respect is dubious.

A second category of phylogeny is derived primarily from the male internal genitalia (e.g. Roberts, Dirsh, Descamps, Amédégnato). The most rigorous analysis of genital characters for large numbers of taxa (Amédégnato 1977) was based on phenetic similarity rather than cladistic methodology, and the original data matrix is not available. The resultant phylogenies are however generally in agreement with those derived from molecular data. Numerical phenetic analysis has also been applied to non-genital morphological characteristics to produce a phylogeny of the Orthopteroid orders (Blackith & Blackith 1967), but the number of Caelifera included in the sample was very small.

Molecular approaches to higher level Caeliferan systematics consist to date of a) cladistic analysis of allozyme polymorphism of glycolytic enzymes (Colgan, 1989), again using a very small taxonomic sample, and b) parsimony and distance analysis of a much larger sample of mitochondrial and nuclear ribosomal sequences by the present authors (Flook and Rowell 1997-2000). Perhaps surprisingly, and reassuringly, most of these diverse methodologies produce phylogenies in rough agreement with each other. Originally we analysed the different ribosomal gene sequences separately. Two molecular phylogenies so derived are indicated below (the phylogenies are consensus trees based on parsimony, distance matrix and maximum likelihood reconstructions).

```
        ====== Tridactyloidea                     =============== Tridactyloidea
        |                                         |
     ===|===== Tetrigoidea                        |  ============ Tetrigoidea
      |  |                                        |  |
      |  ====== Eumastacoidea                     |  |  ========= Eumastacoidea
<<===|                                            |  |  |
```

```
      |  ====== Pneumoroidea sensu Dirsh       <<===|  |  |  ====== Pneumoroidea sensu
Dirsh
      |  |                                          ===|  |  |
      ===|  === Pamphagoidea sensu Dirsh               ===|  |===== Trigonopterygoidea
sensu Dirsh
         ===|                                              ===|
            === Acridoidea                                    |===== Pamphagoidea sensu
Dirsh
                                                              |
                                                              ====== Acridoidea
```

12S + 16S mt rRNA gene tree **18S rRNA gene tree**

Figure 5: Molecular phylogeny of Caelifera after Flook and Rowell (1997a, 1998)

The topologies differ in the levels at which they resolve, but the branching order of the Superfamilies is not contradicted in either phylogeny. The mitochondrial data do not resolve well the oldest branches, presumably due to site saturation, whereas the 18S data do not resolve well the youngest branches, due to insufficient divergence. For this reason we subsequently used combinations of these data sets, with appropriate precautions, to achieve a broader resolution. This strategy has now allowed us to resolve the phylogeny of the entire Caelifera at the level of Superfamily.

The resultant tree is the following:

```
     |==================== Tridactyloidea
     |
<<===|  |================= Tetrigoidea
     |  |
     |  |  |============== Eumastacoidea
     |==|  |
        |  |  |=========== Tanaeoceroidea nov
        |==|  |
           |  |=========== Trigonopterygoidea s.n.
           |==|
              |  |======== Pneumoroidea s.n.
              |==|
                 |   |==== Pyrgomorphoidea nov
                 |===|
                     |==== Acridoidea s.n.
```

Figure 6: Combined 18S, 12S and 6S gene tree (Flook et al., 1999, 2000)

These molecular data often support unequivocally one of several schemes previously proposed on morphological grounds. Thus, for example, the basal placing of the Tridactyloids, the relatively close relationship of the Tetrigoids and Eumastacoids, and the placement of the Trigonopterygoids as a separate group between the Eumastacoids and Pneumoroids, have all been previously suggested by some (though not all!) morphologists, and will probably be generally accepted without dissent.

Among our more original findings is the dismemberment of the Pneumoroidea sensu Dirsh, with the resultant superfamily status of the Tanaoceroidea, the placement of the Xyronotidae as the sister family of the Trigonopterygidae and their joint elevation to superfamily status as the Trigonopterygoidea, and the restriction of the Pneumoroidea sensu novo to the sole family

Pneumoridae. These results are supported by very high levels of statistical probability. The data do not as yet allow resolution of the branching order of the Tanaeoceroidea and Trigonopterygoidea.

The other important finding concerns the Pamphagoidea sensu Dirsh. Some morphologists have seen this group as part of the Acridoidea, others considered the differences in genitalia to warrant separate superfamily status; it was however generally accepted that a) they are monophyletic or at least closely related and b) they are primitive with respect to the remaining Acridoidea. The ribosomal sequences however indicate that this group is actually polyphyletic; the Pyrgomorphidae is indeed a monophyletic clade branching off well before the Acridoidea, but the remaining taxa (principally Pamphagidae & Lentulidae) are embedded within the Acridoidea. We have formalized this finding by raising the Pyrgomorphidae to superfamily status, dropping the superfamily Pamphagoidea and redefining the Acridoidea s.n. to include the Pamphagidae & Lentulidae (see 'A Classification of the Caelifera'). The allozyme data of Colgan (1989), which included a pyrgomorphid, are compatible with our proposition, but do not confirm it, as no other pamphagoid sensu Dirsh was included. Recently, however, Eades (2000) has offered new interpretations of the phallic anatomy of pyrgomorphids, pamphagids and acridids which support the new classification.

Classification

The age of the Caelifera and their multiple convergence to common habitats make their morphological classification difficult below the level of the superfamily. For the past 50 years most weight has been placed on the internal genitalia, especially those of the male sex. These are effectively never available in fossil material: the palaeontological classifications, as in most insect orders, are founded principally on wing venation (Kukalova-Peck, 1991).

Modern authors have usually divided the living Caelifera on morphological grounds into 7 higher taxa, which we here treat as superfamilies (see **Figure 4** above). The majority of living Caelifera belong to the family Acrididae of the Acridoidea. The difficulties in Orthopteran taxonomy have been discussed by Rentz (1991, p. 378) who remarks: "There are many disparate classifications of the orthopteroid insects (or positions thereof) at the present time. The overriding theme is the escalation of the rank of categories above the tribal level. The lack of congruence among authors contributes to considerable instability. Readers should consult Dirsh (1975) for the extreme of these views and Kevan (1982) for a synthesis of the classifications." The most disputed superfamilies have traditionally been the Pamphagoidea, which some authorities regard as insufficiently separated from the Acridoidea to merit independent status, and the Eumastacoidea, which may or may not include the family Proscopiidae. The position of these taxa is discussed in the Discussion of Phylogenetic Relationships, and the accessory page 'A Classification of the Caelifera' provides a proposal for a classification down to the subfamily level which takes in account the results of recent morphological and molecular analyses.

Additionally, there are two Permian/Mesozoic fossil caeliferan taxa, the *Locustopseidae and the *Locustavidae, each sometimes given Superfamily rank, but by others (e.g. Gorochov 1995) grouped as Superfamily *Locustopsoidea. These families are defined only on the basis of wing venation (trifurcate MA and a branched MP+CuA1 in the forewing, branched MA in the hindwing). At least the former family may be simply an assemblage of primitive forms and contain the early representatives of several of the modern groups.

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Information on the Internet

- Orthopterist's society homepage
- The Orthoptera Species File Online (a taxonomic database of the world's orthopteroid insects)
- Grasshoppers of Florida

Title Illustrations

- **Figure 1**. Agriacris tricristata (Acridoidea)
- **Figure 2**. Thericles zebra (Eumastacoidea)
- **Figure 3**. Tetrigoidea sp.

Photographs © C.H.F. Rowell

Scientific Name	Agriacris tricristata
Comments	Acridoidea
Copyright	© 1996 C.H.F. Rowell

Scientific Name	Thericles zebra
Comments	Eumastacoidea
Copyright	© 1996 C.H.F. Rowell

Scientific Name	Tetrigoidea
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About This Page

Hugh Rowell
hrowell@datacomm.ch
Zoology Institute, University of Basel, Rheinsprung 9, Basel 4051, Switzerland

Paul Flook
paul.flook@gcg.com
Genetics Computer Group, 575 Science Drive, Madison, WI 53711, USA

Correspondence regarding this page should be directed to Hugh Rowell at hrowell@datacomm.ch

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- Content changed 23 March 2001

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Phasmida

Phasmids

Erich Tilgner

- Timema
- Euphasmida (stick & leaf insects)

Classification from Bradler (1999), Kristensen (1975), and Tilgner et al. (1999)
Containing group: Neoptera

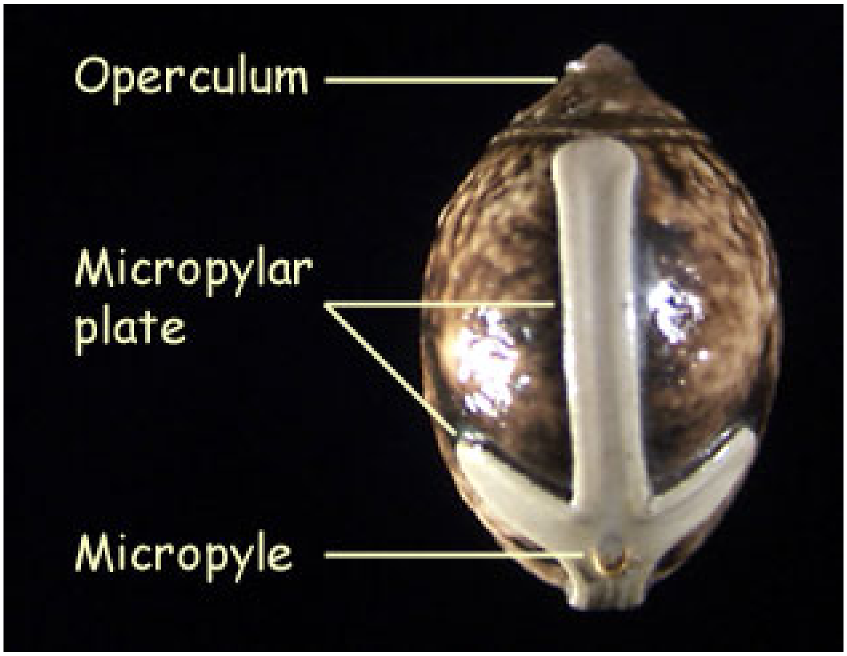
Introduction

Phasmida are terrestrial, nocturnal, phytophagous insects found in nearly all temperate and tropical ecosystems (Günther, 1953). Scientists have described over 3,000 species (Bragg, 1995), yet this figure is uncertain since some taxon names are synonyms, and many new species have not been formally described.

Characteristics

Phasmida are variable in appearance, ranging from relatively generalized forms, to some that are wonderful mimics of sticks and/or leaves. They display varying degrees of brachyptery, and can be winged or wingless. The tarsi have three articles in *Timema* Scudder and five in other Phasmida. Cerci are composed of one article, except for adult males of *Timema* which have a lobe on the right cercus.

Sexual dimorphism is usually extreme: the males are smaller and more gracile than the females. Reproduction is typically sexual, but parthenogenesis occurs frequently. The egg capsule is distinctively shaped, possessing a lid called the operculum and a micropylar plate (Sellick, 1997). Eggs are large and oftentimes highly sculptured resembling plant seeds. They are laid singly, and are dropped, flicked, buried, glued to a surface, or riveted to a leaf. Some species that drop the eggs rely on ants to disperse them in a process analogous to myrmecochory (Windsor et al., 1996). The entire life cycle from egg to adult can take from several months to several years depending on the species.



Egg capsule of *Extatosoma popa*. The nymph escapes by popping off the operculum. Photograph copyright © 2001, Erich Tilgner.

Phasmida possess several unique anatomical features that distinguish them from other Neoptera and indicate they are a monophyletic group (see Tilgner et al., 1999). For example:

- All possess a pair of exocrine glands inside the prothorax (in a few species, these glands can discharge an irritating, tear gas-like spray used for defense).
- The intestine has unique filament bearing glands.
- The dorso-ventral muscles of the abdomen are numerous, short, and arranged in parallel.
- Males of many species possess a unique sclerite termed the vomer. This structure is located above the genitalia and permits the male to clasp the female.

Discussion of Phylogenetic Relationships

Timema is hypothesized to be the sister group to the remainder of Phasmida (Kristensen, 1975, Bradler 1999, Tilgner et al. 1999), termed Euphasmida by Bradler (1999). *Timema* lack the autapomorphies of Euphasmida and possess traits found in other more distantly related Neoptera (Tilgner et al. 1999). No formal phylogenetic analysis has been published testing this hypothesis, but at least two independent studies are currently underway.

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Title Illustrations

Scientific Name	Timema dorotheae
Location	Hualapai Mountains, Arizona
Specimen Condition	Live Specimen
Sex	female
Copyright	© 2001 David R. Maddison

Scientific Name	Heteropteryx dilatata
Specimen Condition	Live Specimen
Sex	Female
Life Cycle Stage	nymph
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About This Page

The author thanks Katja-Sabine Schulz and David R. Maddison for converting this page into the correct format for the Tree of Life. Tatiana Kiselyova kindly provided a review of this work.

Erich Tilgner
etilgner@bugs.ent.uga.edu
413 Biological Sciences Building
Department of Entomology
University of Georgia
Athens, GA 30602
USA

Correspondence regarding this page should be directed to Erich Tilgner at etilgner@bugs.ent.uga.edu

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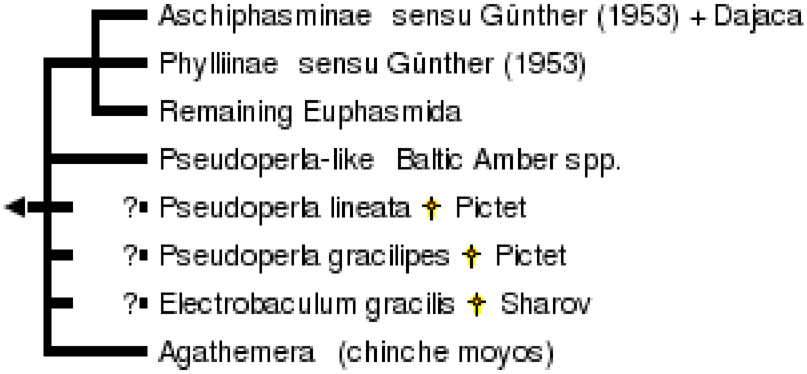
Stick & Leaf Insects

Erich Tilgner



Bradler (2000), Tilgner (2000, unpublished data)
Containing group: Phasmida

Introduction

Euphasmida are commonly referred to as stick and leaf insects. Exquisitely camouflaged, many species look like twigs and may have the appearance of being covered by lichens, mold, bird feces, or moss. The leaf-like forms usually bear a striking resemblance to foliage, exhibiting leaf veins, mildew spots and even apparent insect feeding damage.

Their primary means of avoiding predators is crypsis. If discovered, they either play dead (catalepsy), or they try to scare the predator with a startle display which can include wing flashing, leg kicking, or spastic motion. Some species also release an irritating "tear gas-like" spray when disturbed (see Eisner et al. 1997). In addition, many Euphasmida can purposely lose some of their legs to help free them from a predator's grasp. If this occurs during the immature stages, they can regenerate the lost limbs during successive molts.

Compared to other insects, Euphasmida are large, and a few are gigantic. Several species measure over 200 mm in length (Brock 1999), and the worlds' largest extant terrestrial arthropod is the Euphasmida *Phobaeticus serratipes*, with one documented female measuring 555 mm (Seow-Choen 1995). Since Euphasmida are wonderful looking insects, relatively easy to rear in captivity, they are popular as pets and for displays at zoological gardens (Seiler et al. 2000).

Characteristics

Their tarsi possess five articles unlike *Timema* which have three. The cerci are simple being composed of one article. With the exception of the enigmatic genus *Agathemera*, Euphasmida possess some elongation of the body segments, and the mesothorax is usually elongated.

Euphasmida are hypothesized to be a monophyletic group because of several unique anatomical features they exhibit (Tilgner et al., 1999). For example:

- They have a cusp instead of a grinding lobe on the mandible
- The lateral plates of the prothorax are fused
- Internally, the prothorax has rudimentary sternal projections for muscle attachment.
- The last thoracic segment is fused to the first abdominal segment
- The proventriculus of the intestine is lacking teeth

Discussion of Phylogenetic Relationships

Bradler (2000) hypothesized that the endemic South American genus *Agathemera* is the sister group to the remainder of Euphasmida. This hypothesis is supported by the fact that the ventral muscles of the abdomen of Agathemera span the length of each segment. Other characters suggest *Agathemera* is a basal taxon. For example, the salivary ducts form a tube that opens into the hypopharynx. This condition is rarely found in Euphasmida, where most species have the ducts separate, but it is characteristic of Timema. In addition, the mesothorax is not elongated.

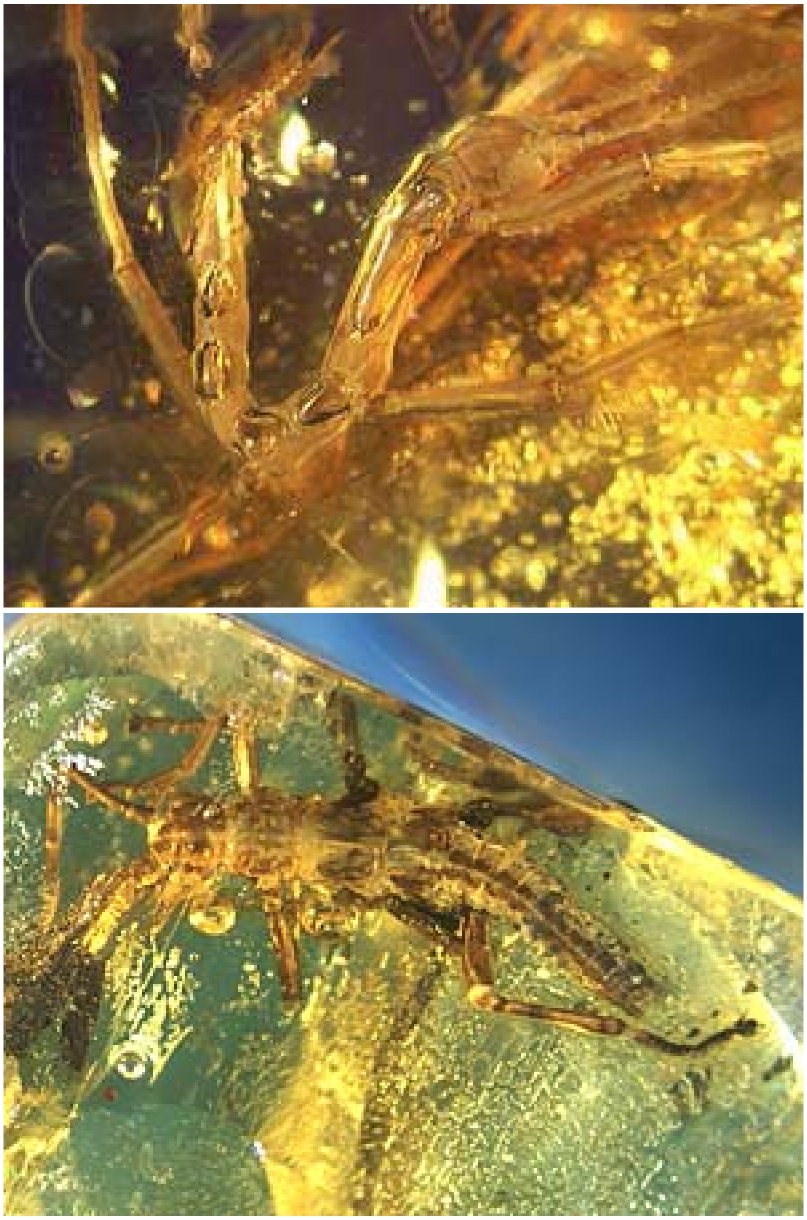
Of the remaining Euphasmida, two putatively monophyletic groups can be recognized in Günther's (1953) classification. The first clade consists of the subfamily Aschiphasmatinae sensu Günther combined with *Dajaca*, a genus classified in the subfamily Pseudophasmatinae by Günther. *Dajaca* are wingless, but in all other respects typical Aschiphasmatinae. The second clade consists of the Phylliinae sensu Günther. The phylogenetic relationship of these two proposed monophyletic groups to the remainder of Euphasmida (both extinct and extant) is not known at this time.

The relationship of *Electrobaculum gracilis* and of the species of *Pseudoperla* to *Agathemera* and other Euphasmida is uncertain. These extinct species are similar to *Agathemera* in that their mesothorax is not elongated. Their abdominal musculature cannot be examined, however, making their placement ambiguous. The remaining extinct species have features indicating they belong to the clade with the remaining Euphasmida, but no obvious synapomorphies link them with any group of extant species.

Fossil Record

Tilgner (2000) has recently provided a review of the Phasmida fossil record, and concluded that they are not an ancient clade of Insecta. The oldest

Euphasmida fossils date to 49-44 million years ago. They are from Grube Messel (Darmstadt, Germany) and Clarno Nut Beds (Oregon, USA). Oligocene and Miocene fossils are known from Florissant shale (Colorado, USA), Baltic, and Dominican Republic amber.



Fossil euphasmid specimens. Left (top): A nymph of a Euphasmida in Dominican Republic amber. Right (bottom): A nymph of *Pseudoperla lineata* fossilized in Baltic amber. Photographs copyright © 2001, Erich Tilgner.

Euphasmida feed almost exclusively on the leaves of Angiosperms. Their phylogenetic and morphological diversification was probably due to an ability to exploit resources and new niches provided by these plants as they dominated terrestrial ecosystems during the later part of the Cretaceous Period and Cenozoic Era.

Note on Common Names

A stick insect is any Euphasmida that is tubular and has a greatly elongated body. Leaf insects are flattened and look like leaves. Many Euphasmida do not fit neatly into either the stick or leaf category, and it is best to refer to them simply as phasmids.

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- Iona & Leigh's Homepage (Information on rearing Phasmida, and a photograph archive)
- Mark Watson's Stick Insect Page
- The Orthopterists' Society
- Phasmids in Cyberspace
- The Phasmid Study Group
- Insectos de Chile, Chilean Insects, a collection by Pedro Vidal (Information on Agathemera)
- The Stick Insects (Phasmida) of South Africa. Compiled by P.D. Brock
- Guide to the stick and leaf insects of New Guinea. By Heinz van Herwaarden.
- Werkgroep PHASMA
- Biology of Phasmids
- Phasmids - adults and detailed pictures of eggs
- Phasmatodea: Bildatlas der Eier. Scanning electron microscope pictures of phasmid eggs.
- Les Phasmes. Cedric's Insect Page
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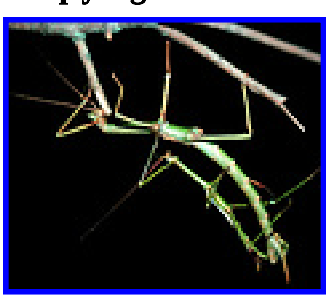
- Insect world
- A Guide to the Stick Insects of Australia

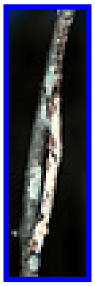
Title Illustrations

Scientific Name	Phyllium bioculatum
Comments	a typical leaf insect
Copyright	© 2001 Erich Tilgner



Scientific Name	Aplopus

Comments	undescribed species, mating pair, male is below female
Specimen Condition	Live Specimen
Sex	male and female
Copyright	© 2001 Erich Tilgner



Scientific Name	Oxyartes spinosissimus
Comments	a stick insect that has the appearance of being covered by lichen
Specimen Condition	Live Specimen
Copyright	© 2001 Erich Tilgner

About This Page

The author thanks Katja-Sabine Schulz and David R. Maddison for converting this page into the correct format for the Tree of Life. Tatiana Kiselyova kindly provided a review of this work.

Erich Tilgner
etilgner@bugs.ent.uga.edu
413 Biological Sciences Building
Department of Entomology
University of Georgia
Athens, GA 30602
USA

Correspondence regarding this page should be directed to Erich Tilgner at etilgner@bugs.ent.uga.edu

- First online 29 August 2001

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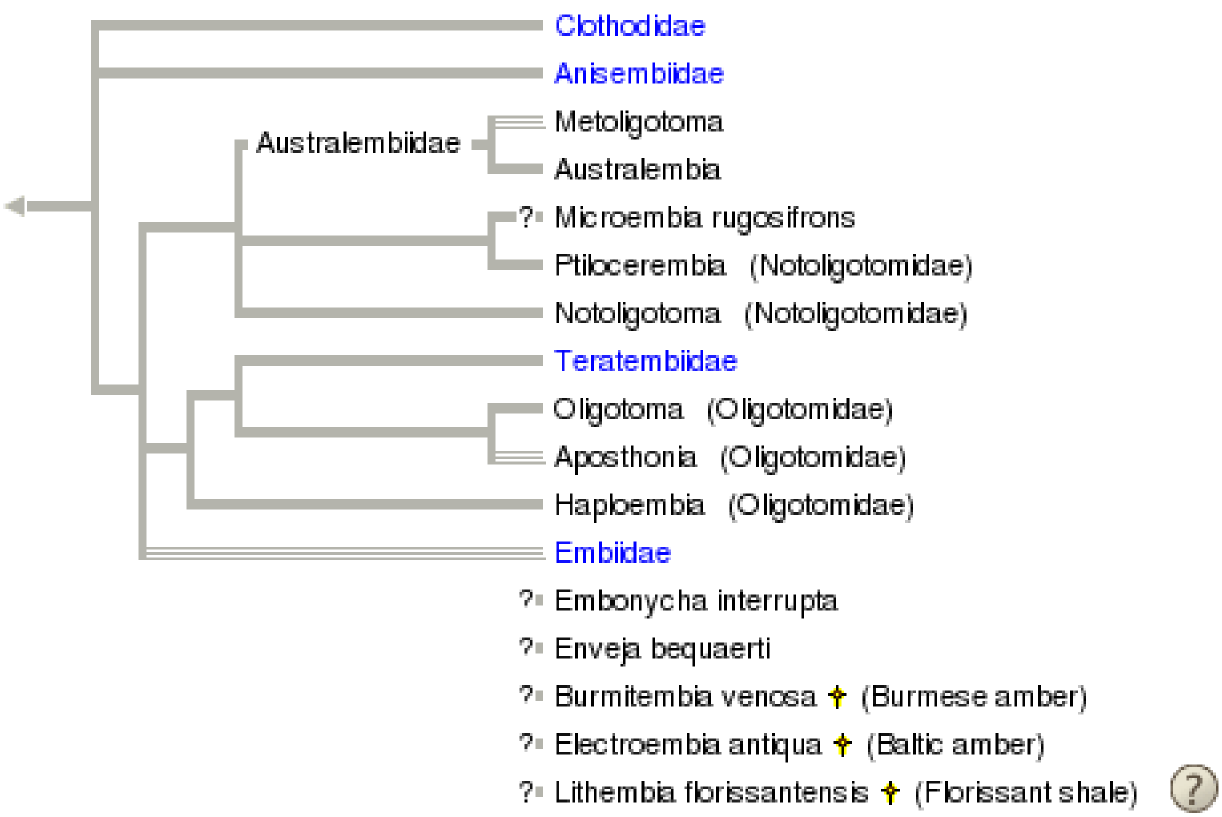
Web spinners



Relationships after Szumik (1996, 1997).

Containing group: Neoptera

Introduction

Oligocene to Recent, with controversial records from the Lower Permian.

embios -lively

Characteristics

- foretarsus modified with silk glands
- live in silken tubes
- wings very flexible; with blood sinus in radius (RBS)
- wingless females
- highly asymmetrical male genitalia

In addition, web spinners exhibit brood care.

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- World List of Extant and Fossil Embiidina. Edward S. Ross, California Academy of Sciences.
- Checklist of South African Embiidina

Title Illustrations

Scientific Name	Embiidina
Copyright	© 1995 David R. Maddison

Scientific Name	Haploembia solieri
Location	Lake Co., California, U.S.A.
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Copyright	© 2005 Alex Wild

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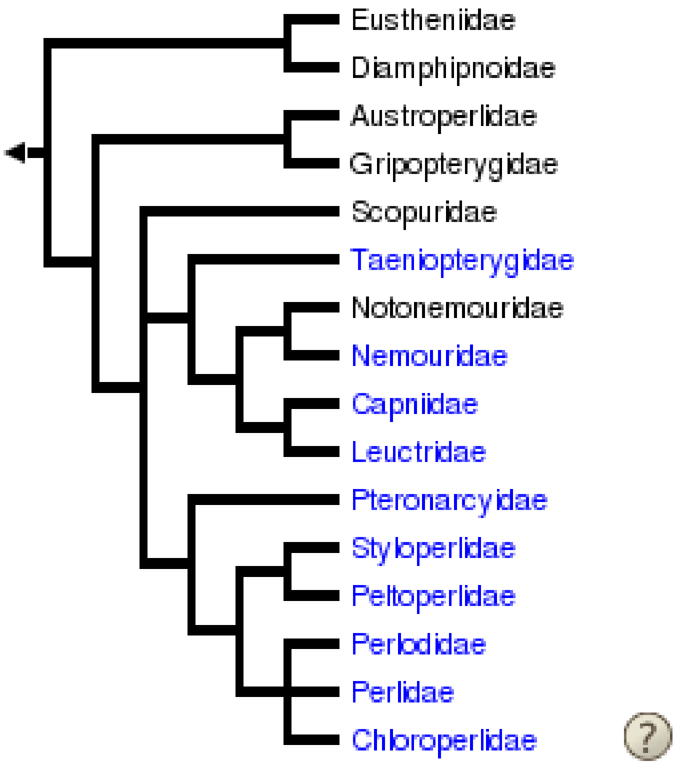
Plecoptera

Stoneflies

C. Riley Nelson



Containing group: Neoptera

Introduction

The Plecoptera (stoneflies) are a small order of exopterygote insects of about 2000 species worldwide. The order has a long, but rather fragmented, fossil record extending back to the early Permian. These Permian fossils can be rather easily contained in the living suborders, Arctoperlaria and Antarctoperlaria. The modern families are clearly identifiable among specimens from the Baltic amber, which is of Miocene age (38-54 million years ago) as well as a few other compression fossils.

The nymphs of stoneflies dwell in aquatic habitats, although there are some species in the southern hemisphere which spend much time on damp land. In general the preferred habitat is rocky streams with a noticeable current, but there are species that live in sandy places. Cold lakes and ponds are also suitable habitats in the north and at high altitudes. We know far less about lakes as habitats than we do about streams and rivers. In running water the usual nymphal habitats are rocky, stony or gravel substrata, and there are more species in cooler, swifter water. Many studies have shown that the various species are each to be found in particular situations. For instance, large Perlidae and Perlodidae are usually found on and under large stones. Chloroperlidae tend to occur in gravel while Pteronarcyidae, and Nemouridae are most frequently encountered in leaf packs.

Finally, it should be stressed that because stoneflies depend upon cool, well-oxygenated water for their nymphal development, they are very susceptible to human abuse of water courses. Any effluent that reduces the oxygen content of the water quickly extirpates them. Even quite minor pollution sources such as farm drainage can elimate stoneflies from nearby streams. Also clearing the land or impoundment or water courses, both of which raise the summer temperature of the water, can eliminate stoneflies from the habitat. Plecoptera, then, as a whole serve as indicators of healthy streams and rivers.

Characteristics

Stoneflies are easily recognized by a few simple characters. They have three segmented tarsi but their hind legs are not modified for jumping to the extent of Orthoptera such as crickets and grasshoppers. They have long filiform antennae at least half length of the body. The cerci are generally long as well, especially in the aquatic nymphs. The wings are almost always present but are sometimes very short. They are folded horizontally back over the body. These characters help distinguish them from Dermaptera and Embioptera which they superfically resemble and to which they are probably closely related.

The immatures are variously called larvae, or nymphs or naiads, but are most frequently referred to as nymphs. All nymphs are aquatic, and resemble the adults in many respects. They also have three-segmented tarsi. The nymphs always have long cerci and never a third central tail or median caudal filament. Gills, if they have them, can occur on various parts of the thorax and abdomen and are composed only of filaments, not plates.

Discussion of Phylogenetic Relationships

Both Zwick (1973) and C. H. Nelson (1984) list Nemouridae and Notonemouridae as sisters. This is an interesting arrangement because the nemourids are uniquely northern hemisphere in distribution and the notonemourids are uniquely southern hemisphere in distribution. This is the only pattern of this sort at the family level (and below!) in Plecoptera. Nemouridae + Notonemouridae is then placed as sister to Capniidae + Leuctridae.

The Pteronarcyidae form a monophyletic group which is most closely related to the Peltoperlidae + Styloperlidae clade (Uchida & Isobe 1989). These three families plus the Perloidea (Perlidae + Perlodidae + Chloroperlidae) have paraglossae and glossae of approximately equal length, and have been called the Systellognatha (sensu Uchida & Isobe 1989).

Pteronarcyids, styloperlids, and peltoperlids (Pteronarcyoidea, sensu Uchida & Isobe 1989), however, are more bland in coloration than the predatory systellognaths (Perloidea sensu Uchida & Isobe 1989) as nymphs. The Pteronarcyoidea are herbivorous throughout their aquatic lives. In contrast, the three perloidean families are all carnivores, at least as mature nymphs. The predatory behavior is a synapomorphy for the Perloidea and a symplesiomorphy for the Pteronarcyoidea.

The relationship of peltoperlids with other stonefly families has been in question since their initial recognition. Zwick (1973) placed the family as the sister group to Subulipalpia (Perlidae, Perlodidae, and Chloroperlidae) with synapomorphies of: 1, body stout, head prognathous, cockroach-like nymphal body form, and 2, male cercal segments fused. Additional apomorphic features which suggest that the family is monophyletic include: 1, nymphal coxae with flap-like lobe (Claassen 1931); 2, nymphal thoracic sterna enlarged into prominent plates, and 3, molar area of nymphal mandibles with pectinate surface (Stark & Stewart 1981). Stark and Stewart (1981) proposed that the family is more closely related to Pteronarcyidae than the carnivorous Subulipalpia based on: 1, nymphal lacinia tridentate; hemispherical, dorsally flattened eggs; and 3, nymphal tergum 10 with apical spine-like process.

The chloroperlids, along with the perlids and perlodids, form a monophyletic trichotomy which has defied splitting despite numerous attempts to determine which family is the nearest sister to which other family. Zwick (1973) listed the chloroperlids as sister to the perlids and cited the synapomorphies for this scheme as having the sternal coxal rotator muscles reduced and having having attachment of muscle I ism 22 shifted from the tip of the furcal arm to near the base (his Fig. 16b). C. H. Nelson (1984) found no resolution to the trichotomy using characters derived from Zwick (1973) and additional characters he explored using numerical cladistic analysis.

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Information on the Internet

- Pictures of stoneflies
- General discussion from England
- North American Stonefly List
- Rolling Stonefly Newsletter
- Nuisance
- Checklist of South African Plecoptera
- Plecoptera Collection of the Siberian Zoological Museum

Title Illustrations

Scientific Name	Triznaka signata, Perlesta decipiens
Specimen Condition	Live Specimen
Life Cycle Stage	Triznaka signata adult, Perlesta decipiens nymph
Copyright	© 1996 C. Riley Nelson

About This Page

I thank Noel Hynes for graciously granting access to the manuscript from which the Introduction and References were distilled.

C. Riley Nelson
rileynelson@byu.edu
Department of Zoology
Brigham Young University
Provo, UT 84602-5255

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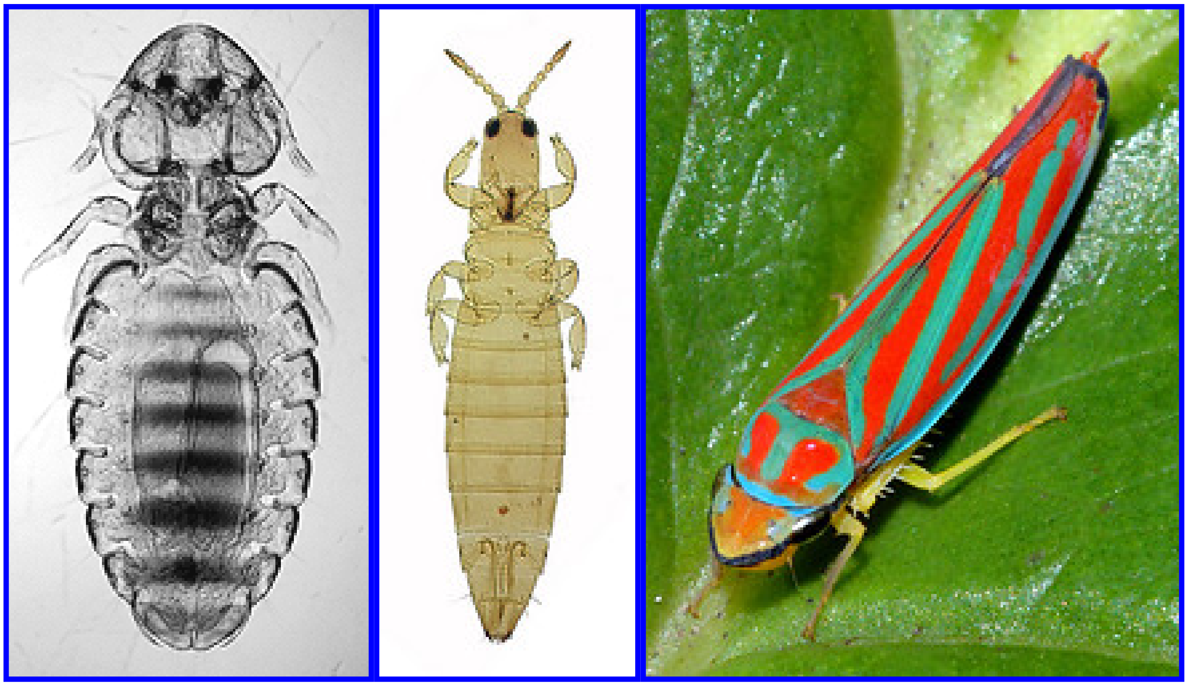
Hemipteroid Assemblage

Bugs, Thrips, and Lice



- Psocodea (lice and booklice)
- Thysanoptera (thrips)
- Hemiptera (bugs, cicadas, whiteflies, aphids, etc.)

Containing group: Neoptera

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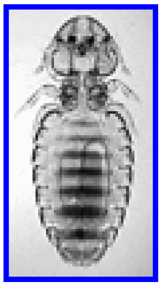
Title Illustrations



Scientific Name	Bovicola bovis
Specimen Condition	Dead Specimen
Copyright	© 1996 David R. Maddison

Scientific Name	Aptinothrips rufus
Acknowledgements	Photograph courtesy InsectImages.org (#0019006)
Specimen Condition	Dead Specimen
Copyright	© John W. Dooley, USDA APHIS PPQ

Scientific Name	Graphocephala coccinea
Location	Maryland, United States
Acknowledgements	Courtesy InsectImages.org (#1366056)
Specimen Condition	Live Specimen
Life Cycle Stage	adult
Copyright	© Susan Ellis

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Psocodea

- Psocoptera (book lice) (monophyly uncertain)
- Phthiraptera (lice)

Containing group: Hemipteroid Assemblage

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Thysanoptera

Thrips

- Terebrantia
  - Merothripidae
  - Uzelothripidae
  - Aeolothripidae
  - Adeheterothripidae
  - Heterothripidae
  - Thripidae
  - Fauriellidae
- Tubulifera
  - Phlaeothripidae

Classification from Mound and Heming (1991), in Insects of Australia

Containing group: Hemipteroid Assemblage

Introduction

thysanos - fringe; pteron -wing.

Characteristics

Derived characteristics:

- asymmetrical mouthparts with right mandible lost
- pretarsus with protrusible "bladder", which balloons out as leg makes contact with the ground.
- wing linear with long marginal setae
- two or three quiescent, pre-imaginal instars

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Information on the Internet

- CSIRO Entomology - Thysanoptera
- Laurence Mound's Research
- ThripsNet

Title Illustrations

Scientific Name	Frankliniella occidentalis
Location	Northern Sierra Nevada, California, USA
Comments	Western flower thrips
Specimen Condition	Live Specimen
Copyright	© 2004 Alex Wild

Scientific Name	Ceratothrips frici
Location	San Mateo County
Comments	Dandelio thrips intercepted by John Nelson on grasses
Acknowledgements	Photograph courtesy InsectImages.org (#0019007)
Specimen Condition	Dead Specimen
Copyright	© John W. Dooley, USDA APHIS PPQ

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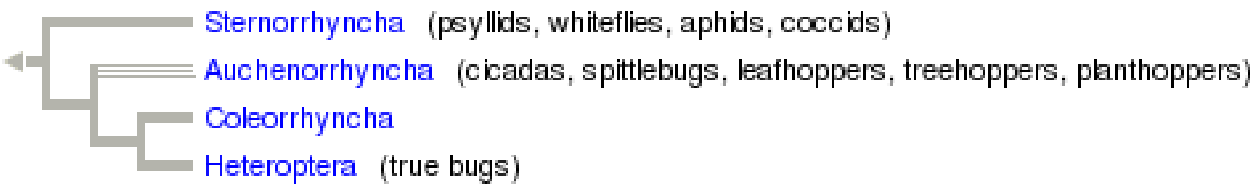
  - Sternorrhyncha

Hemiptera

True bugs, cicadas, leafhoppers, aphids, etc.



Tree based upon Schuh (1979), Carver et al. (1991), and Wheeler et al. (1993), and von Dohlen and Moran (1995). Note that Auchenorrhyncha may not be monophyletic (see Campbell et al. 1994, 1995; Sorensen et al. 1995).

Containing group: Hemipteroid Assemblage

Introduction

Hemisys - half; pteron - wing; referring to the fact that many of its members have the basal half of the fore wings thicker than the distal half.

Permian to Recent.

Characteristics

Derived characteristics:

- mandiblulary and maxillary stylets coadapted, containing alimentary and salivary canals, enclosed in segmented labium

Other characteristics:

- holocentric chromosomes

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Zrzavy, J. 1992. Morphogenesis of antennal exoskeleton in Heteroptera (Insecta): From phylogenetic to ontogenic pattern. Acta Entomologica Bohemoslovaca 89(3): 205-216.

Title Illustrations

Scientific Name	Aphidomorpha
Location	U.S.A.: Michigan
Comments	Aphids (Sternorrhyncha) on milkweed, U.S.A.: Michigan
Copyright	© 1995 Joseph L. Spencer

Scientific Name	Cicadidae
Location	Costa Rica: La Selva
Comments	A cicada (Auchenorrhyncha)
Copyright	© 1995 Joseph L. Spencer

Scientific Name	Heteroptera
Location	Costa Rica
Comments	A true bug
Copyright	© 1995 Michael Singer

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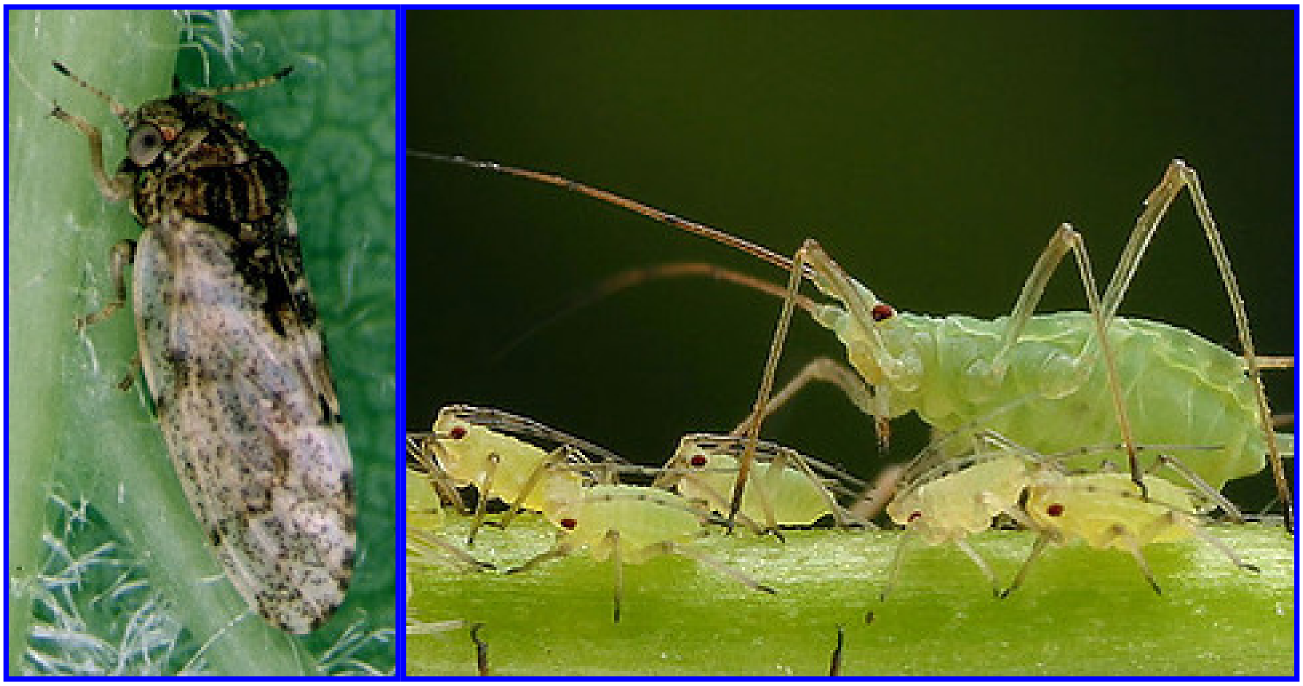
Sternorrhyncha



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    - Calophyidae
    - Phacopteronidae
    - Homotomidae
    - Carsidaridae
    - Triozidae
- Aleyrodoidea
    - Aleyrodidae
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- Coccoidea
    - Margarodidae
    - Ortheziidae
    - Phenacoleachiidae
    - Pseudococcidae
    - Eriococcidae
    - Dactylopiidae
    - Kermesidae
    - Aclerdidae
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    - Asterolecaniidae
    - Cerococcidae
    - Lecanodiaspididae
    - Coccidae
    - Kerriidae
    - Phoenicococcidae
    - Conchaspididae

- Beesoniidae
- Halimococcidae
- Diaspididae

Classification from Carver, Gross, and Woodward (1991), in Insects of Australia.
Containing group: Hemiptera

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Information on the Internet

- ScaleNet: A Database of the Scale Insects of the World

Title Illustrations

Scientific Name	Pachypsylla celtidismamma
Acknowledgements	Courtesy InsectImages.org (#1325046)
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Copyright	© Whitney Cranshaw, Colorado State University

Scientific Name	Acyrthosiphon pisum
Location	Davis, California, USA
Comments	Pea aphids
Specimen Condition	Live Specimen
Copyright	© 2003 Alex Wild

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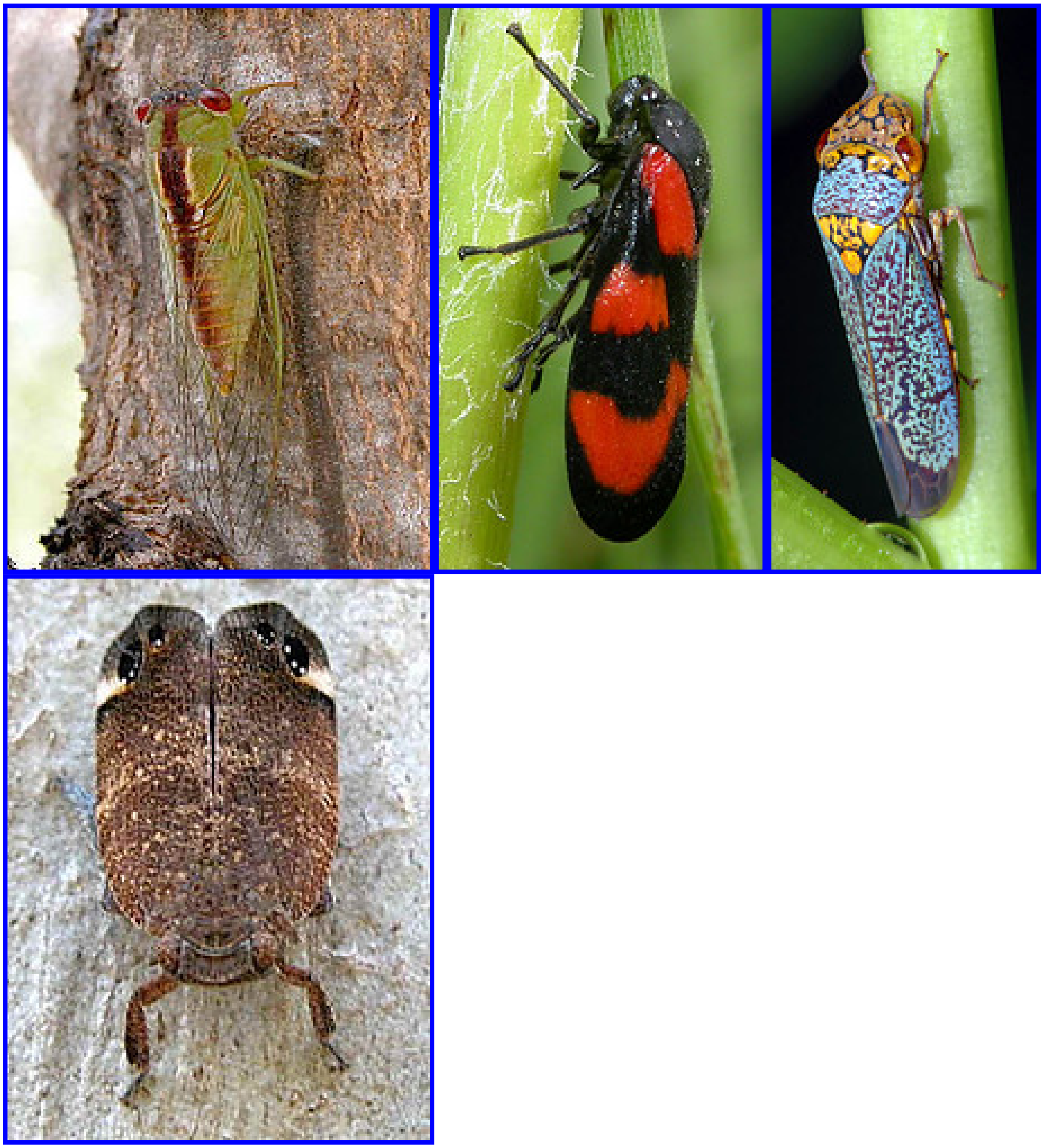
  - Cicadoidea
  - Fulgoromorpha
  - Membracoidea

Auchenorrhyncha

Cicadas, spittlebugs, leafhoppers, treehoppers, and planthoppers



- Cicadomorpha
  - Cicadoidea (cicadas, tettigarctid cicadas)
  - Cercopoidea (froghoppers, spittlebugs)
  - Membracoidea (leafhoppers, treehoppers)
- Fulgoromorpha (planthoppers)

Classification from Carver, Gross, and Woodward (1991), in Insects of Australia
Containing group: Hemiptera

Discussion of Phylogenetic Relationships

This group may be paraphyletic, with the Coleorrhyncha and Heteroptera derived from within it. See the papers by Campbell et al. (1994, 1995), Sorensen et al. (1995), and von Dohlen and Moran (1995).

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- Periodical Cicadas: An on-line database (University of Connecticut)
- University of Michigan Cicada Pages
- Fulgoromorpha Lists on the Web
- NAVIS: Songs of Cicadas
- Cicadas - Australian Museum Online
- Cicadas in Ancient Greece
- Checklist of the Cicadas of South Africa
- The Cicadas of Central Eastern Australia
- Cicadas in Chinese Folklore
- Phantastic songs of the S.E. Asian cicadas

Title Illustrations

Scientific Name	Cicadetta oldfieldi
Location	Brisbane, Australia
Comments	Thin-striped wattle cicada
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Size	20mm
Copyright	© Peter Chew

Scientific Name	Cercopis vulnerata
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Size	9mm
Copyright	© 2001-2005 Benoit Martha

Scientific Name	Oncometopia nigricans
Location	Maryland, United States
Acknowledgements	Courtesy InsectImages.org (#1366063)
Specimen Condition	Live Specimen
Life Cycle Stage	adult
Copyright	© Susan Ellis

Scientific Name	Platybrachys vidua
Location	Brisbane, Australia
Comments	Planthopper
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Size	15mm
Copyright	© Peter Chew

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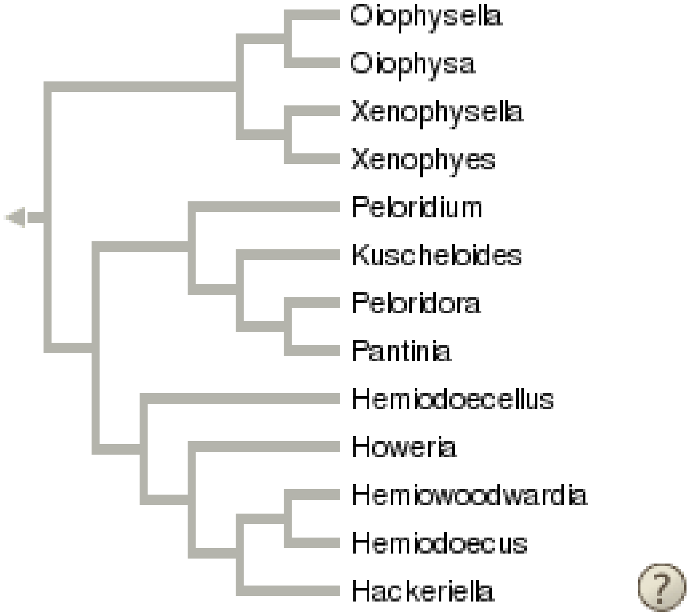
Coleorrhyncha

Peloridiidae



Relationships after Popov & Shcherbakov 1996.
Containing group: Hemiptera

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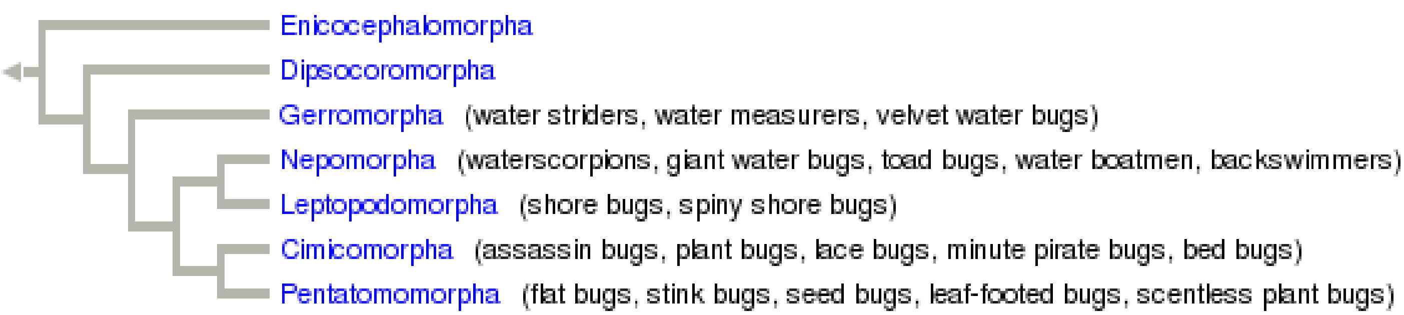
  - Pentatomomorpha

Heteroptera

True bugs



Tree based upon Schuh 1979, Wheeler et al. (1993)

Containing group: Hemiptera

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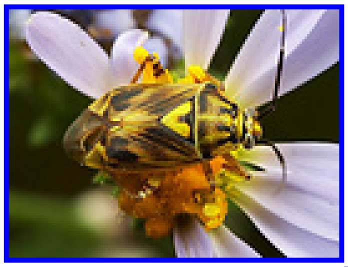
Information on the Internet

- Checklist of the Heteroptera of Europe
- Checklist of the Heteroptera of New Zealand

Title Illustrations

Scientific Name	Sigara nigrolineata
Location	Slovenia
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Copyright	© Andrej Gogala



Scientific Name	Lygus sp.
Location	Northern Sierra Nevada, California, USA
Comments	Tarnished plant bug
Specimen Condition	Live Specimen
Copyright	© 2004 Alex Wild

Scientific Name	Ischnodemus sabuleti
Location	Germany
Specimen Condition	Live Specimen
Life Cycle Stage	Nymph
Copyright	© 2003 Jürgen Deckert

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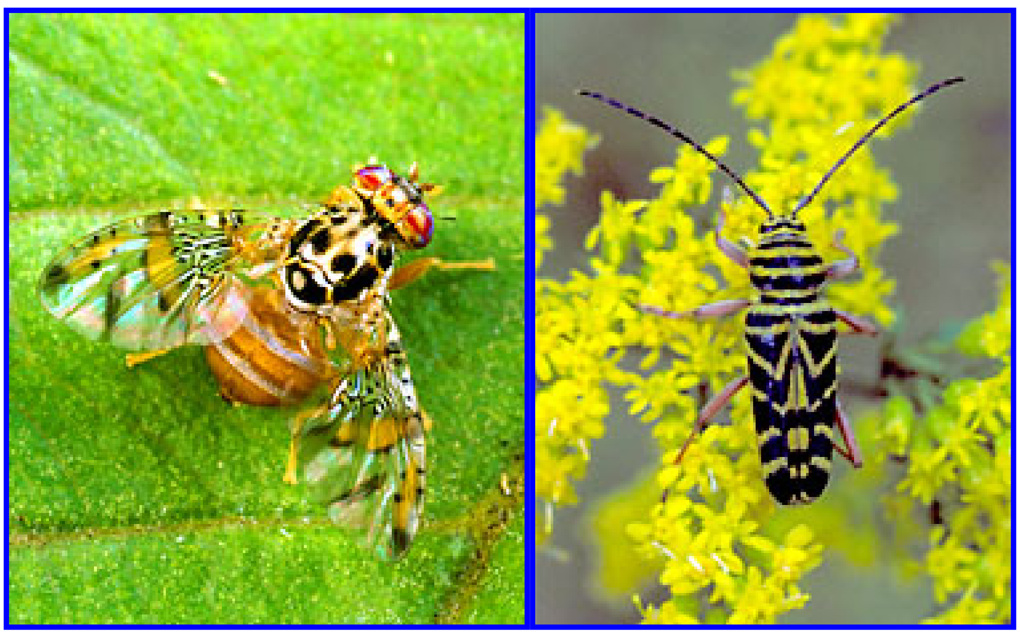
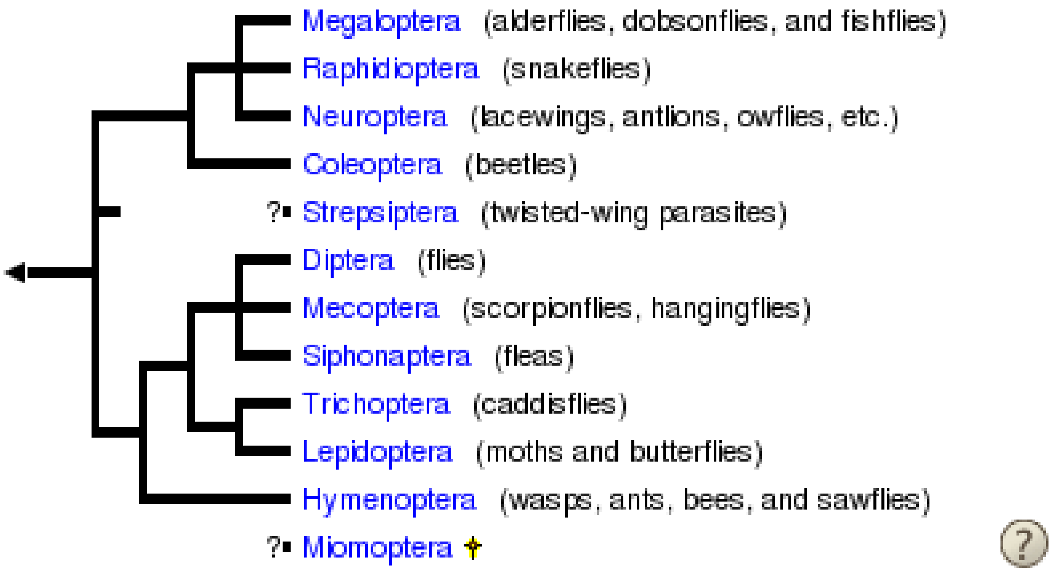
Endopterygota

Insects with complete metamorphosis





Containing group: Neoptera

Introduction

Endopterygotes are those insects with distinctive larval, pupal, and adult stages. Their name (endo = within, pterygos = wing) refers to the fact that in later immature stages the wing buds are not evident externally, but instead the future wing tissues are entirely internallized; they make their first external appearance in the penultimate (pupal) stage. In contrast, other winged insects (for example, bugs) have external wing buds in instars before the penultimate.

Another name for this group is Holometabola, refering to the "complete metamorphosis" of the species; that is, the dramatic changes between larval, pupal, and adult stages.

Four of the five largest orders of insects belong to this group (Coleoptera, Hymenoptera, Lepidoptera, and Diptera).

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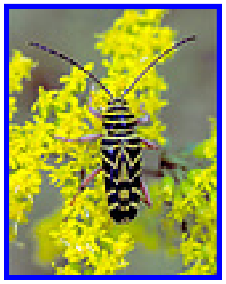
Wootton, R. J. 2002. Design, function and evolution in the wings of holometabolous insects. Zoologica Scripta 31:31-40.

Title Illustrations

Scientific Name	Ceratitis capitata
Comments	medfly
Creator	Photograph by Scott Bauer
Acknowledgements	courtesy USDA Agricultural Research Service
Specimen Condition	Live Specimen
Sex	Male



Scientific Name	Megacyllene robiniae
Comments	Locust borer
Acknowledgements	Courtesy InsectImages.org (#0488008)
Specimen Condition	Live Specimen
Copyright	© John H. Ghent, USDA Forest Service

Scientific Name	Aleiodes indiscretus, Lymantria dispar (2)
Comments	Aleiodes indiscretus wasp parasitizing a gypsy moth caterpillar (Lymantria dispar).
Creator	Photograph by Scott Bauer
Acknowledgements	courtesy USDA Agricultural Research Service
Specimen Condition	Live Specimen

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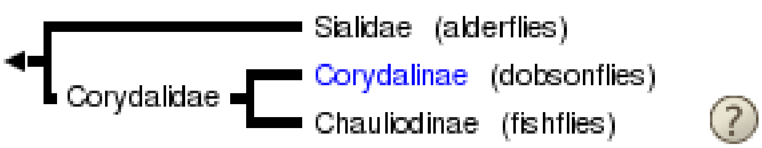
Megaloptera

Alderflies, dobsonflies, fishflies

Atilano Contreras-Ramos



Tree represents standard accepted classification.
Containing group: Endopterygota

Introduction

The order Megaloptera, formerly considered a suborder (Sialodea) of Neuroptera, is generally considered to be among the most primitive of the holometabolous insect orders. It contains two families, the Sialidae (alderflies) and the Corydalidae, the latter subdivided into the Corydalinae (dobsonflies) and the Chauliodinae (fishflies). The fauna of Megaloptera consists of about 300 extant species worldwide (New and Theischinger 1993). A list of all megalopteran genera is available here.

A typical dobsonfly male with elongated mandibles. Corydalus imperiosus Contreras-Ramos (Corydalidae: Corydalinae), Misiones, Argentina. Photograph copyright © 1997, Atilano Contreras-Ramos

Like Ephemeroptera, Odonata, Plecoptera, and Trichoptera, the order Megaloptera is entirely aquatic, i.e., all--or nearly all--megalopteran species have at least one aquatic stage. Adults of Corydalidae are particularly noteworthy for their frequently large size, and, in many species of the genera Corydalus and Acanthacorydalis, for the extremely elongated mandibles of adult males. Adult fishflies and dobsonflies are generally nocturnal and secretive, while alderflies are diurnal yet not too frequently collected. At the right place and time of the year (e.g., near the edge of clean lakes in Minnesota, U.S.A., around June), however, it is possible to find individuals of the fishfly Chauliodes rastricornis Rambur congregating under lights, or aggregates of alderflies on vegetation during day time.

Characteristics

Adults of Megaloptera can be identified by the enlarged and fan-folded anal area of their hind wings (Borror et al. 1989). Those of Corydalidae are large (forewing longer than 15 mm, wingspan up to 180 mm), pale yellowish to brownish or spotted black, with ocelli, and their 4th tarsal segment is simple; while those of Sialidae are small (forewing 15 mm or less), dark brown to gray and black (sometimes with orange spots on the head), lack ocelli, and their 4th tarsal segment is bilobed.

Larvae are elongate, moderately flattened, prognathous, have a distinct labrum, and measure 10-90 mm when mature. Mouth parts are of the chewing type, well developed. Larvae bear lateral abdominal filaments (on segments 1-8 in Corydalidae, and 1-7 in Sialidae) and either a pair of anal prolegs (Corydalidae) or a single caudal filament (Sialidae). Members of the subfamily Corydalinae also possess tufts of accesory tracheal gills under the lateral filaments of segments 1-7 (Evans and Neunzig 1996, Theischinger 1991).

Life History

Oviposition

Megaloptera adults lay their egg masses on rocks, tree trunks, leaves, and other substrates adjacent to water, and the young larvae fall or crawl into the water shortly after hatching. Sialid egg masses are single layered, whereas corydalids lay their eggs in egg masses of one to five layers (Evans & Neunzig 1996).

There does not seem to be a clear preference for oviposition substrates in Neotropical dobsonflies. Nevertheless, a certain selectivity for substrates may be hard to determine in some cases, as egg masses of Chloronia, Corydalus, and Platyneuromus are quite similar (whitish, chalky, coin size). Canterbury (1978), reports a general selection of vegetation hanging over the water for the oviposition of eastern North American sialids, however, some species preferred leaves, and other species oviposited on twigs or branches.

Larval Habitats

Typically, alderfly larvae are associated with lentic habitats (sediments of lakes and depositional zones of streams), while corydalid larvae (hellgrammites) mostly occur in lotic environments (riffles and other erosional zones, from small mountain streams to large rivers). Some Australian fishflies are known from swamps (Theischinger 1991), whereas North American Chauliodes are typically associated with lakes, ponds, and swamps (Cuyler 1958). Canterbury (op. cit.) found that some Sialis species seemed to be confined to one type of aquatic habitat (e.g., small clear streams, larger streams, small woodland ponds, or bays and inlets of lakes). Hayashi (1989), as well, points out a possible habitat seggregation between Parachauliodes japonicus (MacLachlan) and Protohermes grandis (Thunberg) larvae in Japanese streams. The former apparently restrict themselves to shallow edge waters, where they can utilize abdominal respiratory tubes in the event of an oxygen decrease, while the latter prefer the central part of riffles (larvae having gill tufts, but lacking respiratory tubes). On the same token, Geijskes (1984) found in Suriname an apparent preference of Corydalus nubilus Erichson and C. affinis Burmeister to large open rivers, while C. batesii MacLachlan and Chloronia hyeroglyphica (Rambur) seemed to be restricted to small shaded creeks.

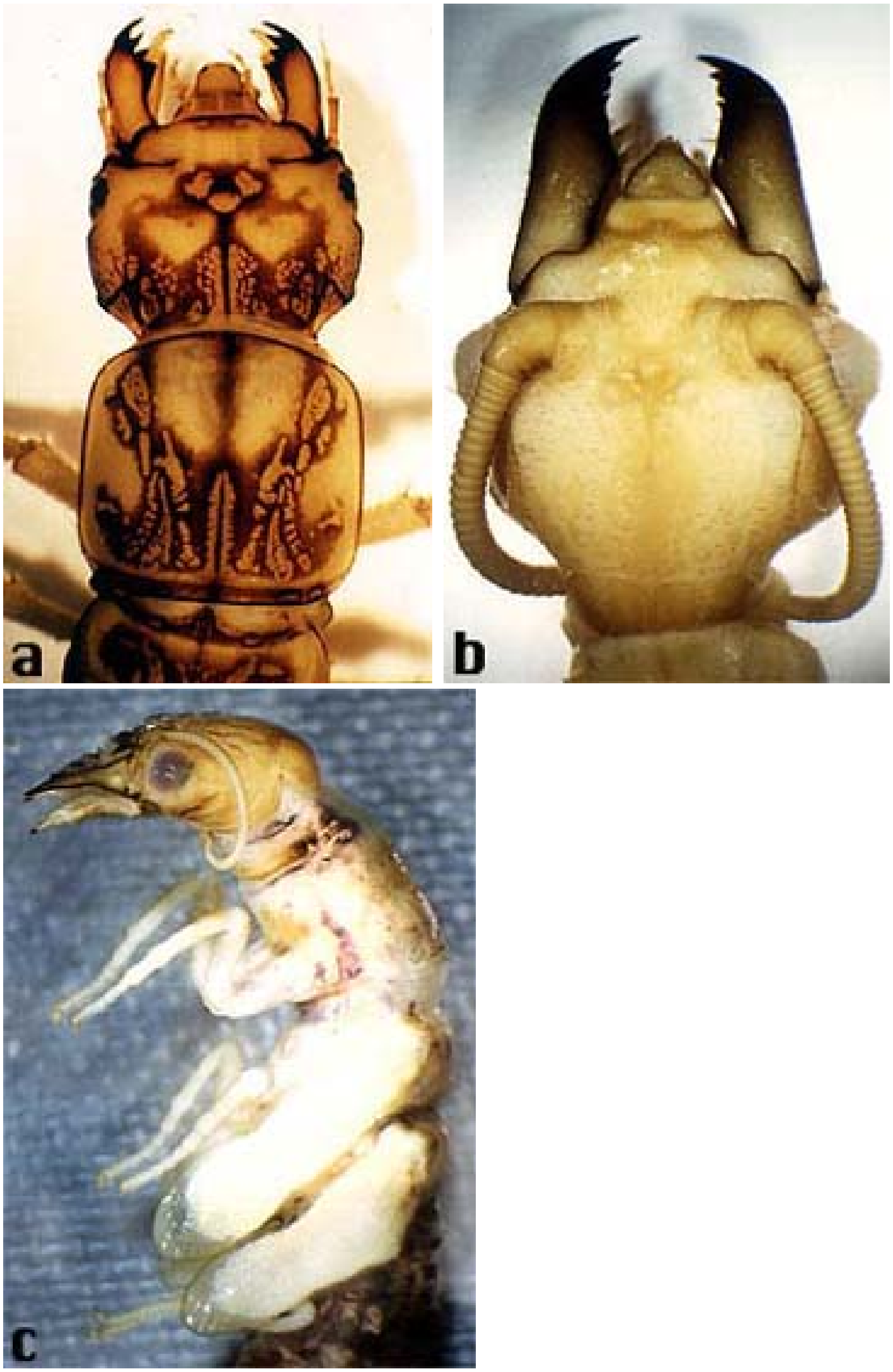
Recent findings indicate the occurrence of Chauliodes and Sialis larvae in "unusual" habitats, such as tree holes and purple pitcher plants (Fashing 1994, Hamilton et al. 1996, Pittman et al. 1996). This is additional evidence of this group's larval endurance to cope with potentially inhospitable conditions. This is the case in other fishfly species, such as Neohermes californicus (Walker), whose first instar larvae bury into the substrate of dry intermittent streams during summer in California, remaining in cells until rains reappear in late fall and streams flow once again (Smith 1970).

Larval Development

Alderflies are very difficult to find in tropical climates (Henry et al. 1992). Although they occur through most of the world (with the exception of much of Africa), life histories of species of temperate climates are better known. In Europe, the life cycle of Sialis lutaria L. has been found to take from one to two years and even three years in high altitude lakes (Dall 1989), whereas in North America Sialis species have shown life cycles of one to two years (Azam & Anderson 1969, Pritchard & Leischner 1973). There are 10 larval instars in the development of Sialis under natural conditions (New & Theischinger 1993, Evans & Neunzig 1996).

Evans (1972) estimated that development of western North American fishflies might take from two (Neohermes) to four and five years (Dysmicohermes, Orohermes, Protochauliodes), while Hayashi (1989) estimated a two-year larval period for Parachauliodes japonicus. He (1988a) also determined a two to three year larval period for Protohermes grandis (Thunberg).

Bowles (1990) cites studies on Nearctic Corydalus cornutus (L.) that report life histories of one (southern latitudes) to five years (northern latitudes), the larvae having 10-12 instars. Hayashi (1994) found larval periods that varied from one to three years in Japanese Protohermes, period length depending strongly on water temperature.



Immature Megaloptera. a. larva of Platyneuromus soror (Hagen) (Corydalidae, Corydalinae), Nuevo León, Mexico; b. male pupa of Corydalus cornutus (L.) (Corydalidae, Corydalinae), Alabama, USA; c. female pupa of Nigronia fasciatus (Walker) (Corydalidae, Chauliodinae), Alabama, USA. Photographs copyright © 1997, Atilano Contreras-Ramos

Larval Feeding Ecology

Megalopteran larvae are generalist predators and, at least in captivity, scavengers. Stewart et al. (1973) found larvae of black flies (Diptera: Simuliidae) and net spinning caddisflies (Trichoptera: Hydropsychidae) as the main items in the diet of the dobson fly Corydalus cornutus (L.) hellgrammites in a Texan river, but 17 other aquatic insect groups (in addition to individuals of its own species!) were also eaten. Hayashi (1988b) found larvae of the Japanese fish fly Protohermes grandis to feed on a wide variety of benthic macroinvertebrates including mayflies, stoneflies, and chironomids, showing some degree of cannibalism as well. Similar patterns have been observed for alder flies, although a certain specificity has been detected. For instance, the North American Sialis itascae Ross was observed to prey mostly on ostracods, even when several other prey were available (Lilly et al. 1978, cited by New & Theischinger 1993).

Pupae and Adults

When mature, the larvae leave the water and build a chamber under a rock or log, not too far from the aquatic habitat. In these chambers they spend several days as prepupae (generally about a week), then they molt and become decticous and exarate pupae which are capable of limited movement, including a strong defensive bite. After several more days (8-24 days in Corydalidae, 5-8 days to about a month in Sialidae; New & Theischinger 1993) the adults emerge and the life cycle is completed.

Adults are short-lived and generally do not feed, though they may drink water or sweet solutions. Parfin (1952) recorded an average of eight days for the adult longevity of Nearctic Corydalus cornutus. Mexican adult Platyneuromus soror (Hagen) lived for up to a week in captivity, however actual life span might be longer in nature since specimens had been collected with black light; moreover damage on wings and antennae points out injuries due to confinement conditions (Contreras-Ramos 1999a).

Reproductive Biology

Mating and courtship behavior are better known in Sialidae than in Corydalidae. Several studies on Sialis (New & Theischinger 1993) reported reciprocal signalling, which implies a vertical vibration of the abdomen by males and females. Vibrations allow mutual recognition of species and sex. In some dobsonflies (e.g., Corydalus texanus Banks and Platyneuromus soror), males may use female attractant scents from eversible glands near the genitalia (between 8th and 9th abdominal segments and under the 9th sternum; Evans 1972; Contreras-Ramos 1998, 1999a).

Corydalus males fight when encountering each other (Evans 1972, Parfin 1952). Platyneuromus males only display a threatening position (mandibles open) but do not fight (Contreras-Ramos 1990). Premating behavior in Corydalus involves touching of antennae between male and female while facing one another, as well as male wing fluttering (Parfin 1952, Evans 1972). In Platyneuromus soror, males actively pursue females, at the same time fluttering their wings and lifting their genitalia (10th tergites) above the level of the wings in an "arrogant" position (Contreras-Ramos 1999a).

Fertilization involves the transfer of a gelatinous spermatophore (Hayashi 1992, 1993). This reproductive strategy might cause low levels of sexual selection ("female choice" pattern, sensu Eberhard 1985), resulting in a rather conservative morphology of male genitalia (Contreras-Ramos 1998).

Discussion of Phylogenetic Relationships

The monophyly of Megaloptera is generally accepted, however adult synapomorphies remain obscure (New and Theischinger 1993, Kristensen 1991). Boudreaux (1979) suggested the following traits as apomorphies for the order: (i) wing pterostigma secondarily unpigmented, (ii) loss of the terminal bifurcations of the main veins, (iii) larvae aquatic (the embryonic limb buds become leglike structures into which respiratory tracheae appear to penetrate), (iv) larval maxillary stipes elongated, as in the adult condition. Similarly, the monophyly of each family (and so the sister group relationship of Chauliodinae and Corydalinae) has not been demonstrated explicitly through a phylogenetic analysis. It is, however, a general assumption in current classifications.

Boudreaux (1979) proposed the following features as derived. Corydalidae: (i) enlarged jugal area with a prominent jugal bar in the hind wing, (ii) hind wing folding among the posterior anal veins (not at the jugal fold as in other endopterygotes and Sialidae). Sialidae: (i) adult gula, cervical region, and the prothoracic sternum secondarily desclerotized, (ii) ocelli lost, (iii) 4th tarsomeres strongly bilobed, (iv) claspers of the male genitalia reduced, and (v) larval pygopods (anal prolegs) lost.

Since Sialidae appears to be the group with more specializations, such as the secondary desclerotization of the gular region and the reduction of structures in the male genitalia, among others, there should be caution as to grouping Chauliodinae and Corydalinae on the basis of primitive characters (however this question deserves a thorough phylogenetic analysis of its own).

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- Megaloptera Collection Holdings. California Academy of Sciences.
- Megaloptera Bibliography. North Carolina State University.
- Introduction to Megaloptera (CSIRO)
- Notes on the Neuroptera and Megaloptera of Madagascar and Adjacent Islands

Title Illustrations

Scientific Name	Corydalus peruvianus
Location	Costa Rica
Sex	Female
Copyright	© 1997 Ralph W. Holzenthal

About This Page

Atilano Contreras-Ramos
acramos@uaeh.reduaeh.mx
Universidad Autonoma del Estado de Hidalgo
Pachuca (Mexico)

Correspondence regarding this page should be directed to Atilano Contreras-Ramos at acramos@uaeh.reduaeh.mx

- First online 12 November 1997
- Content changed 14 October 1997

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Raphidioptera

Snakeflies

- Raphidiidae
- Inocelliidae

Containing group: Endopterygota

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Title Illustrations

Scientific Name	Raphidioptera
Location	Del Puerto Canyon, California, U.S.A.
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
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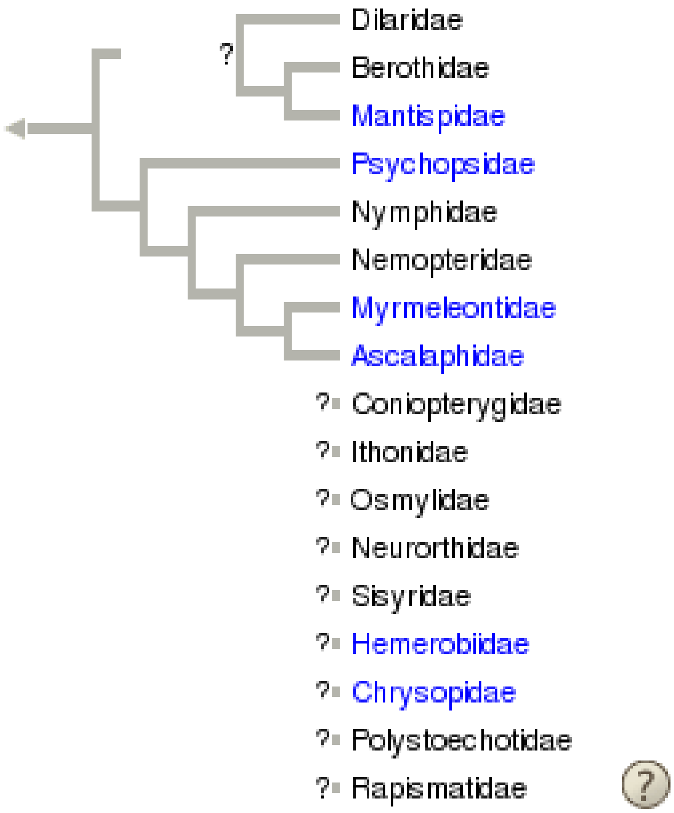
- Myrmeleontidae
- Psychopsidae

Neuroptera

Lacewings, antlions, owlflies, etc.

John D. Oswald



Containing group: Endopterygota

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- NeuroWeb - The Neuropterist' Home Page
- The Antlions and Lacewings (Neuroptera) of South Africa
- The Antlion Pit - a doodlebug anthology
- AntLionFarms.com
- Neuropterida Species in California Entomology Collections
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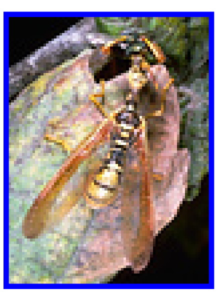

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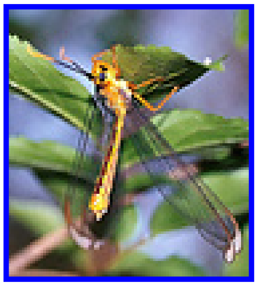
Creator	T. W. Davies
Acknowledgements	Courtesy CalPhotos
Specimen Condition	Live Specimen
Life Cycle Stage	Adult

Copyright	© 1999 California Academy of Sciences



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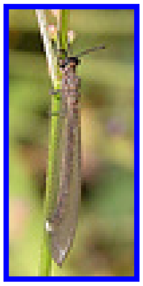
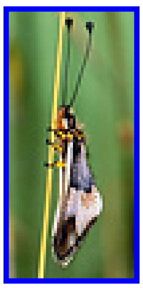
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Copyright	© Peter Chew



Scientific Name	Myrmeleontinae
Location	Bulimba Creek, Wishart, Australia
Comments	Antlion
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
Copyright	© Peter Chew



Scientific Name	Libelloides sp.
Location	Peloponnese, Greece
Comments	Owlfly
Specimen Condition	Live Specimen
Life Cycle Stage	Adult
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About This Page

John D. Oswald
WPODOM1.ENTOMOLOGY.JOSWALD@wpo-smtp-gate.tamu.edu

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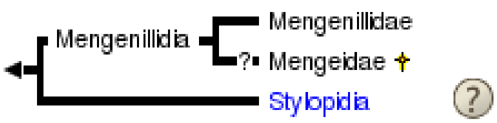
Strepsiptera

Twisted-wing parasites

Jeyaraney Kathirithamby



Relationships after Kinzelbach 1978.
Containing group: Endopterygota

Introduction

Strepsiptera are obligate parasites of insects, with hosts ranging across 7 orders and 34 families. The name of the group is derived from the Greek words for twisted (*streptos*) and wing (*pteron*) and refers to the peculiar twisted wing of the male's hind-wings while in flight. Representatives of the suborder Mengenillidia generally show more primitive characteristics (fig. 1). The Mengenillidae parasitize Thysanura (Lepismatidae), the only known order in the sub-class Apterygota to be attacked by strepsipterans, while Mengeidae are known only from fossil males from Baltic amber. We have very little information about their life history, therefore.

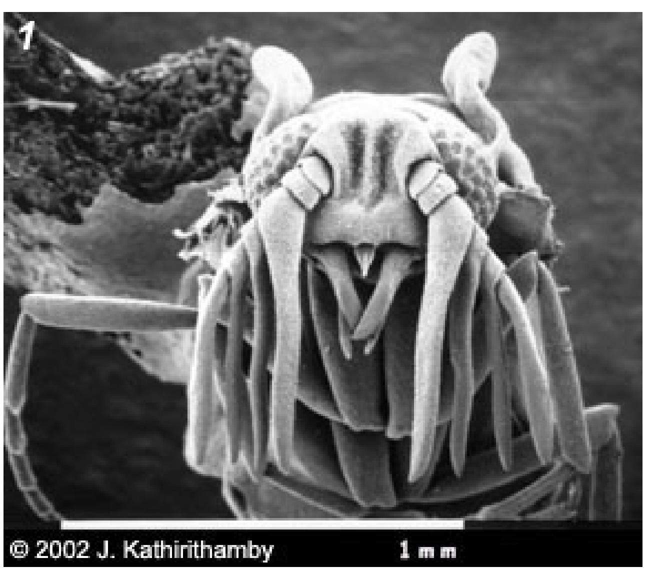


Figure 1. Adult male: *Mengenilla* sp.

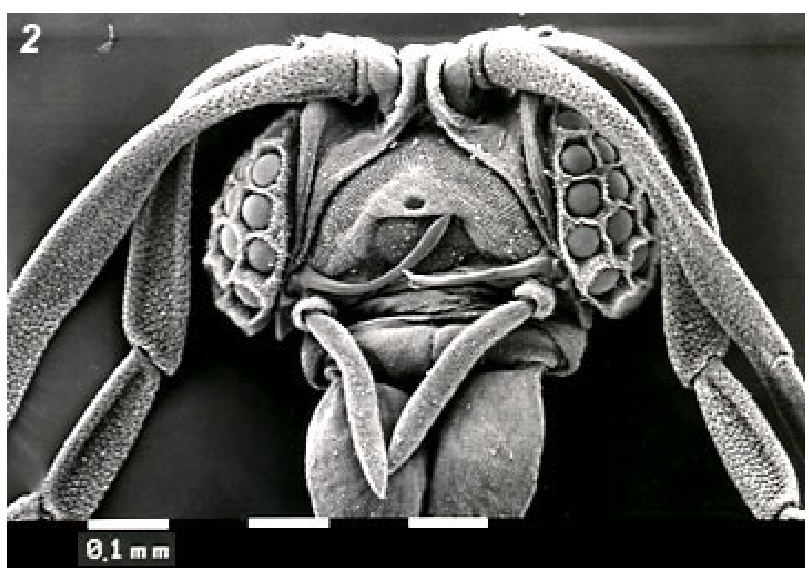
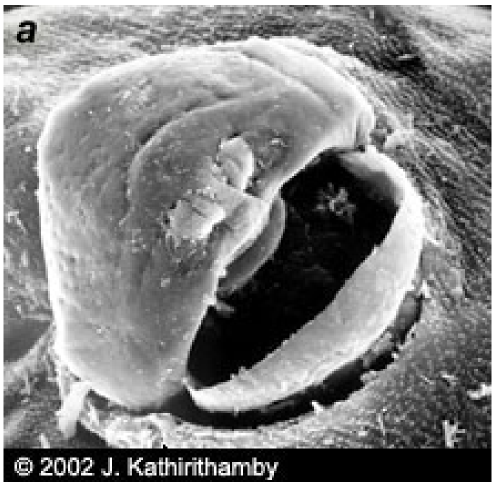


Figure 2. Adult male: *Myrmecolax rossi* Bohart

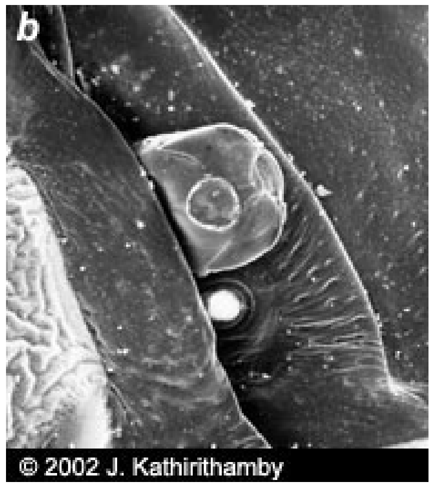
(Mengenillidae) (Northern Territory, Australia). Copyright © 2002 J. Kathirithamby

(Myrmecolacidae) (Queensland & Northern Territory, Australia). From Kathirithamby (1993). Copyright © 1993 CSIRO, reproduced by permission.

Strepsiptera exhibit extreme sexual dimorphism, which is most pronounced in the suborder Stylopidia. Strepsipteran males emerge from the host after endoparasitic pupation in the host. Adult males are free-living, and their sole mission is to find and fertilize a female. They have reduced forewings and fan-shaped hind wings, branched antennae, and raspberry-like eyes (title image and fig. 2); the latter are very unusual among living insects and form a modern counterpart to the structural plan proposed for eyes of trilobites (Kinzelbach 1971, 1990, Kathirithamby 1989, Buschbeck et al. 1999).



a. *Elenchus varleyi* Kathirithamby (Elenchidae). (Queensland, Australia).



b. *Coriophagus rieki* Kinzelbach (Halictophagidae). (Canberra, ACT, Australia)

c. *Dipterophagus daci* (Drew & Allwood) (Halictophagidae). (Queensland, Australia)

Figure 3. Cephalothorax of adult females. Micrographs copyright © 2002 Kathirithamby

Females of the family Stylopidae are neotenic (i.e., they retain juvenile features even in adulthood) and totally endoparasitic in their hosts. They are highly modified morphologically, lacking adult external characteristics such as eyes, antennae, legs, wings and external genitalia (fig. 3). Apart from the adult males, the only free-living stages in this suborder are the viviparous 1st instar host-seeking larvae (fig 4). In contrast, males and females in the family Mengenillidae leave the host at the end of the last larval instar to pupate externally (fig. 5, 6). After eclosion, the females are free-living, with the presence of all other adult characteristics such as eyes, mouthparts, antennae, legs and a ventral genital opening, but with the absence of wings (fig. 7).

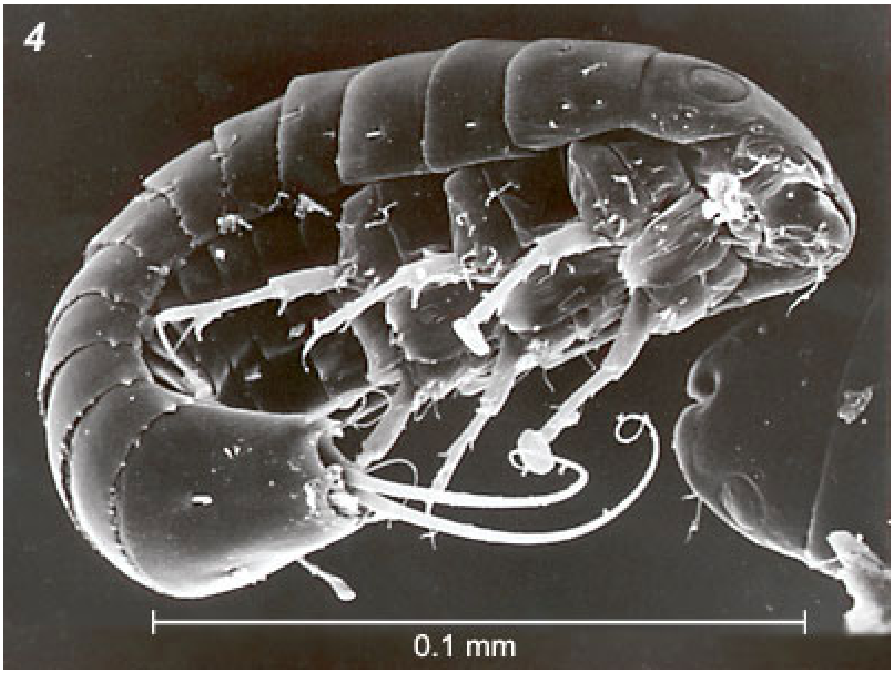


Figure 4. 1st instar free-living larva: *Stichotrema dallatorreanum* Hofeneder (Myrmecolacidae) (Papua New Guinea). From Kathirithamby & al. (1998). Copyright © 1998 Taylor & Francis.

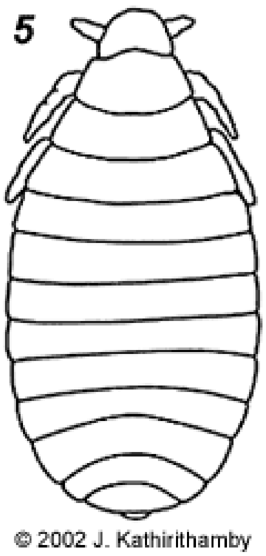


Figure 5. Free-living female pupa: *Mengenilla chobauti* Hofeneder (Mengenillidae)

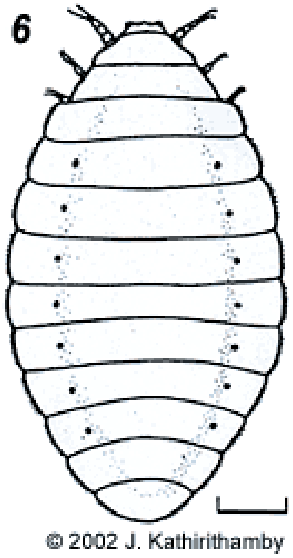


Figure 6. Free-living male pupa: *Eoxenos laboulbenei* De Peyerimhoff (Mengenillidae)

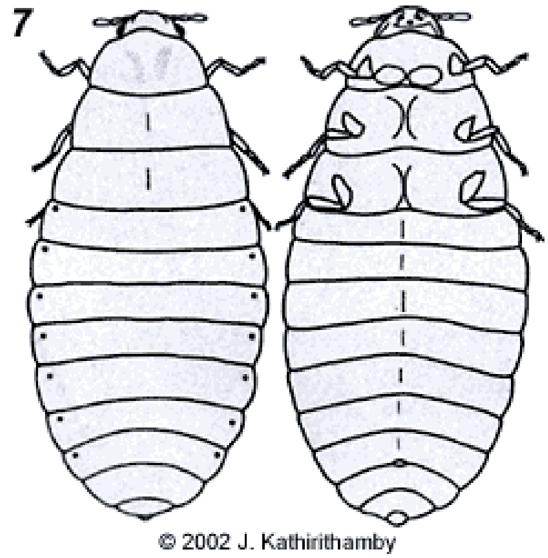


Figure 7. Free-living female of *Eoxenos laboulbenei* De Peyerimhoff (Mengenillidae)

Drawings after Kinzelbach 1971. Copyright © 2002 J. Kathirithamby

The combination of morphological reduction and modification, and the bizarre and unusual life history of Strepsiptera, have puzzled biologists for over two centuries (Rossi 1793; Latreille 1809; Kirby 1802, 1813. 1815; Lamark 1816 Pierce 1909; Crowson 1960, 1981; Arnett 1963; Kinzelbach 1971, 1990; Kathirithamby 1989), and the Strepsiptera's phylogenetic position has been the most enigmatic question in ordinal level insect systematics (the "Strepsiptera problem", Kristensen 1981, see below).

Strepsiptera are cosmopolitan in distribution (Table 1), but are extremely difficult to locate, and one often has to find the host in order to find the female. To date, 596 species of Strepsiptera have been described and many more await description. Many of the described species are of free-living males that have come into traps. At present, since sites have been located where Strepsiptera can be collected, some of the species are being reared in the laboratory. Work on the extraordinary reproductive and developmental biology and behavioural ecology of this group is under way.

Table 1: Geographical distribution of the extant families of Strepsiptera.

Family	Geographical Range					
	Palaearctic	Afrotropical	Australian	Oriental	Neotropical	Nearctic
Mengenillidae	+	+	+	+	-	-
Corioxenidae	+	+	+	+	+	+
Halictophagidae	+	+	+	+	+	+
Elenchidae	+	+	+	+	+	+
Myrmecolacidae	+	+	+	+	+	+
Stylopidae	+	+	+	+	+	+
Bohartillidae	-	-	-	-	+	-
Callipharixenidae	-	-	-	+	-	-

Characteristics

Strepsiptera are characterized by the following synapomorphies:

1. Free-living host-seeking 1st instar larvae, which are produced viviparously by the neotenic female. Several hundred are produced which emerge from the female and seek new hosts. Sexual dimorphism does not exist in the 1st instars. These 1st instars are often known as "triungulin" larvae. This term was initially applied to the Meloidae, because of the presence of three claws on the legs. The term was later extended to the Rhipiphoridae and Strepsiptera, and refers to the active host-seeking larvae. However, morphologically, the 1st instar larvae of Strepsiptera do not resemble the Meloidae. The pulvillus of the 1st pair of legs is disk-like, and slender; single, spine-like tarsi are present on the 2nd and 3rd pair of legs, while there is absence of claws. In addition, the 1st instars have highly serrated tergites and sternites, presumably to enable them to cling to the hosts and/or vegetation while awaiting entry. The head bears antennae, mandibles, and labrium, and the abdominal setae are long, and are about a third or half the body length.
2. The 1st instar larvae moult, on entry into the host, to an apodous 2nd instar. Therefore, all Strepsiptera exhibit hypermetamorphosis (two morphologically distinct larval instars—the 1st larva and subsequent endoparasitic stages).
3. The endoparasitic larvae undergo apolysis without ecdysis (Kathirithamby et al. 1984) whereby the larvae moult but do not shed the old cuticle. It was found that *Elenchus tenuicornis* (Kirby) and *Stichotrema dallatorreanum* Hofeneder have four larval instars

(Kathirithamby 1998).

4. In the male, at the last larval instar, the cuticle is sclerotized to form the puparium (fig. 8) (Kathirithamby 1983).

Figure 8. Male pupa of *Pseudoxenos* sp. (Stylopidae) between sternites of *Odynerus bicolour* Saussure (Hymenoptera).

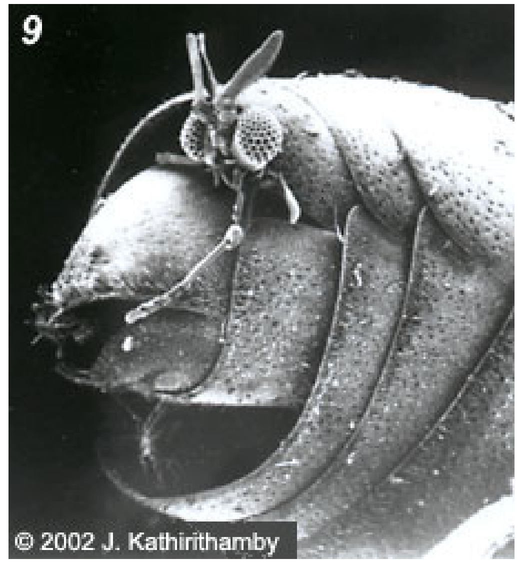


Figure 9. Adult male *Pseudoxenos* sp. (Stylopidae) emerging from puparium in *Odynerus bicolour* Saussure (Hymenoptera).

5. The free-living males have prominent branched antennae and raspberry-like eyes, reduced forewings and large hindwings (title image and fig. 2). They are short-lived, and their sole mission on emergence from the host (fig. 9) is to find and fertilize a female. There is no trochanter on the fore and middle legs, and the metacoxae are fused to the pleurosternum. The male has an aedeagus but no copulatory apparatus, such as parameres.
6. The females are neotenic (fig. 3) and totally endoparasitic in their hosts (except in the family Mengenillidae). The external cuticle on the ventral surface is analogous to the peritrophic membrane (found in the midgut of other insects) in adult females (Kathirithamby 2000). The whole abdominal cavity of the adult female is filled with developing embryos. Fertilization is by haemocoelic insemination, and reproduction is by haemocoelous vivipary.

Discussion of Phylogenetic Relationships

Kinzelbach (1971) divided the Strepsiptera into two suborders (Mengeillidia and Stylopidia) and nine families. Seven of these families are here united in the suborder Stylopidia, which is defined by many shared derived characteristics. The monophyly of this group has recently also been confirmed by Pohl's (2002) analysis of the 1st instar larvae of nearly all extant strepsipteran families.

The family Mengeidae is known only from a few fossil males from Baltic amber, all representing a single species, *Mengea tertiaria* (Menge). *Mengea* shares many plesiomorphic characters with the Mengenillidae, such as:

a. Similar round head capsule
b. Inwardly directed mandibles

c. Presence of abdominal stigmata
d. 5-jointed tarsi
e. Straight aedeagus.

Therefore, the two groups have often been associated with one another (Pierce 1908, 1909, 1918; Ulrich 1927, 1956; Bohart 1941, Luna de Carvalho 1956, 1959 1961, 1967; Kinzelbach 1969a; Riek 1970). Since all of the traits shared by *Mengea* and the Mengenillidae may be plesiomorphic, and there are a few tentative morphological similarities between *Mengea* and the stylopidian family Corioxenidae, Kinzelbach (1971)included the Mengeidae in the Stylopidia. However, in 1978 Kinzelbach placed the Mengeidae in the Mengenillidia. He says the formation of the labrium, free metacoxa, number of antennal joints, wing vein CuP are more plesiomorphic than the Mengenillidae, and the recent Mengenillidae may be thought to be derived from Mengeidae. Since females are unknown it will be regarded as a sister group of the Mengenillidae. Hence the phylogenetic position of the Mengeidae will remain uncertain until additional specimens are found which allow a more detailed analysis of the morphology and life history of this fossil group.

Relationship of Strepsipterans to Other Insects

Strepsiptera are a monophyletic group (Henning 1981). In recent years, four phylogenetic placements of these insects have been proposed:

1. Sister group to the Endopterygota. Kristensen (1991, 1995) noted that the position of Strepsiptera may not be within Endopterygota since:
    - the pupal stage is preceded by a couple of pharate instars (Whiting et al. 1997 interpreted this as the 2nd instar) with external wing buds
    - larval eyes are carried over to the adult stage

    These two characters are plesiomorphic within Endopterygota. However, neither the 2nd instar nor any of the other endoparasitic larval stages in the male have external wing buds (Kathirithamby et al. 1984). The pupal stage in the male begins when the 4th instar larval cuticle is sclerotized to form the puparium (Kathirithamby et al. 1984). Within this puparium there are three pupal instars which have external wing buds. The endoparasitic development in the male is therefore holometabolous. In the neotenic female (except in the Mengenillidae), the pupal stage is lost secondarily (Kathirithamby 2000). The structure of the larval eyes is being investigated (Kathirithamby unpublished).
2. Crowson (1960, 1981) placed Strepsiptera within the coleopteran suborder Polyphaga, as sister to Rhipiphoridae. This theory was based on derived features in rhipiphorids which he said were similar to Strepsiptera:
    - active host-seeking 1st instar larva
    - hypermetamorphosis from a 1st instar larva to apodous endoparasitic larvae
    - flabellate antennae
    - reduced forewings (in some genera)

    The above morphological characters shared by Strepsiptera and Rhipiphoridae have been erroneously interpreted:
    - active host-seeking stage and hypermetamorphosis have arisen once in the Exopterygota and five times in the endopterygota;
    - flabellate antennae are found in many insects;
    - as pointed out by Kathirithamby (1989) and Pix et al. (1993), the reduced forewings in Strepsiptera are neither morphologically nor functionally similar to the elytron in Coleoptera.
3. Handlirsch (1903), Boerner (1904) and Shipley (1904) placed Strepsiptera as a sister group to Coleoptera, and Kinzelbach (1971, 1990) and Kathirithamby (1989, 1991) argued that this placement was based on only one character: posteromotorism (use of the

hind wings for flight). The venational characters supporting the sister group relationship between the Coleoptera and Strepsiptera (Kukalova-Peck and Lawrence 1993) were disputed by Whiting and Kathirithamby (1995).

4. The hypothesis that the Strepsiptera are a sister group to true flies (Diptera) is based on both morphological and molecular evidence, and has been championed by Whiting and Wheeler (1994) and Whiting et al. (1997), but remains controversial.
   - Whiting and Wheeler (1994) published a short note indicating that a phylogenetic analysis of 18S ribosomal DNA suggested that Strepsiptera were related to Diptera. No data or details of the analysis were included in the note, but this information eventually appeared in Whiting et al. 1997. The authors further suggested that the reduced, mesothoracic wings of strepsipteran males may be homologous to the halteres (on the metathorax) of dipterans, and that their presence on different thoracic segments is due to homeotic mutation.
   - Carmean and Crespi (1995), in response, provided an analysis of 13 18S ribosomal DNA sequences, and showed that the branches leading to Diptera and Strepsiptera were both very long. They suggested that the grouping of these taxa in a parsimony analysis of the data might be artifactual, caused by long-branch attraction (Felsenstein 1978).
   - Chalwatzis et al. (1996) analysed 18S rDNA of 19 insect species, and similarly found a grouping of Strepsiptera plus Diptera, even though they used distance methods (with several distance measures) that would be affected by long-branch attraction under different conditions than parsimony methods.
   - Whiting et al. (1997) presented their complete analysis, using parsimony methods, of 85 18S rDNA sequences and 52 28S rDNA sequences, as well as morphological data. This analysis also supported a grouping of Strepsiptera plus Diptera.
   - Huelsenbeck (1997) showed that the data set of 13 18S ribosomal DNA sequences used by Carmean and Crespi (1995), when analysed with maximum likelihood methods, yielded a tree with Strepsiptera as sister to Coleoptera. He suggested that long branch attraction is the cause of the placement of Strepsiptera with Diptera when parsimony methods are used.
   - Rokas et al. (1999) investigated the potential of an intron insertion site as a phylogenetic character. They found that the en homeobox gene of *Stichotrema dallatorreanum* lacks the derived intron insertion shared by representatives of Diptera and Lepidoptera. They thus argued against a close affiliation between Strepsiptera and Diptera.
   - Huelsenbeck (2001) observed that quality and quantity of morphological data available are limited, and that it is molecular data which hold the promise to solving the problem. The two ribosomal genes available, 18S and 28S, produced different placements of Strepsiptera. He states that more molecular data are needed to solve the phylogenetic placement of Strepsiptera.

Therefore the position of Strepsiptera among Insecta is still not solved, but work is being carried out on molecular and morphological data to try and resolve the question of the placement of Strepsiptera. Collaborating laboratories are: Jeyaraney Kathirithamby and Peter Holland (Oxford), John Huelsenbeck (San Diego) and Spencer Johnston (Texas A&M).

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- Strepsiptera. Hans Pohl's Strepsiptera page with many great images.
- The Oxford University Strepsiptera Collection
- Strepsipteran Eyes (Ronald Hoy, Cornell University)
- An insect with 100 eyes has left scientists, well, surprised. 1999 Scientific American exhibit about Buschbeck et al.'s research on the eyes of strepsipteran males.
- Strepsiptera.com

Title Illustrations

Adult male: *Elenchus tenuicornis* (Kirby) (Elenchidae). (Oxford, UK).
Image from Kathirithamby (1989). Copyright © 1989 Blackwell Science.

Scientific Name	Elenchus tenuicornis
Location	Oxford, UK
Comments	x270
Reference	Kathirithamby, J. 1989. Review of the order Strepsiptera. Systematic Entomology 14:41-92.
Specimen Condition	Dead Specimen
Sex	Male
Life Cycle Stage	adult
Copyright	© 1989 Blackwell Science

About This Page

Jeyaraney Kathirithamby
jeyaraney.kathirithamby@zoology.oxford.ac.uk
Department of Zoology
South Parks Road
Oxford OX1 3PS
United Kingdom

Correspondence regarding this page should be directed to Jeyaraney Kathirithamby at
jeyaraney.kathirithamby@zoology.oxford.ac.uk

- First online 24 September 2002

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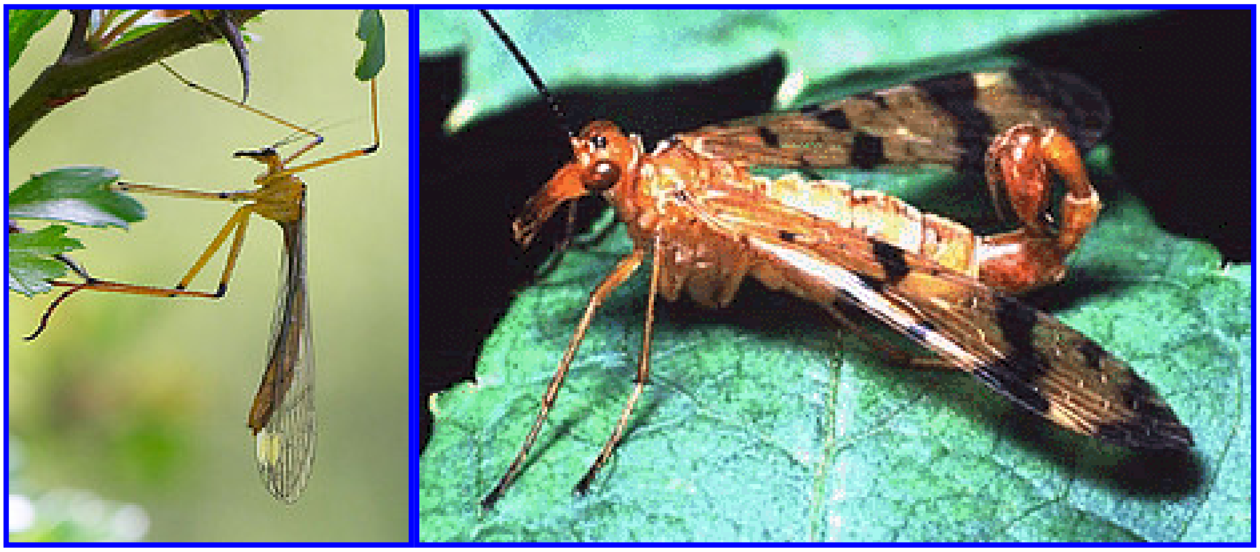
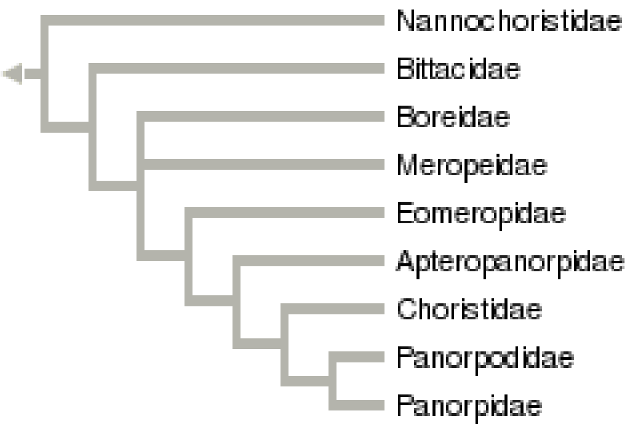
Mecoptera

Scorpionflies and hangingflies





Tree from Willmann (1987)
Containing group: Endopterygota

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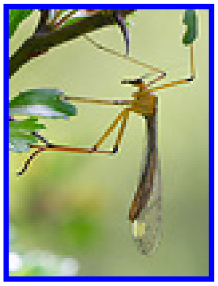
- World Checklist of Extant Mecoptera Species

- Checklist of South African Hangingflies

Title Illustrations



Scientific Name	Bittacus chlorostigma
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Comments	Hangingfly
Life Cycle Stage	Adult
Copyright	© 2005 Alex Wild

Scientific Name	Panorpidae
Copyright	© 1995 Joseph L. Spencer

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Siphonaptera

Fleas

- Tungidae
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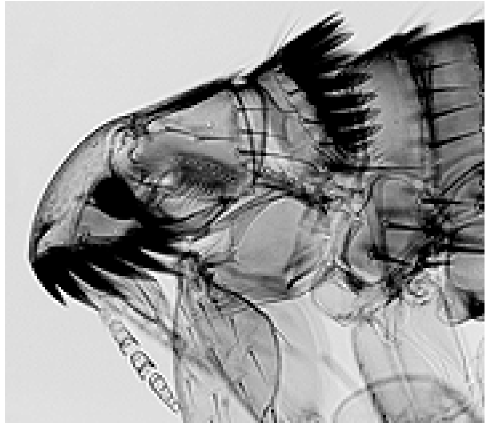
- Vermipsyllidae
- Hystrichopsyllidae
- Coptopsyllidae
- Pygiopsyllidae
- Stephanocircidae
- Macropsyllidae
- Xyphiopsyllidae
- Ancistropsyllidae
- Chimaeropsyllidae
- Ischnopsyllidae
- Leptopsyllidae
- Ceratopsyllidae

Containing group: Endopterygota

Characteristics

Laterally flattened.

Here is the head of Ctenocephalides:



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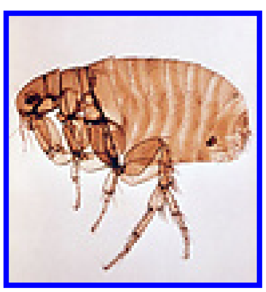
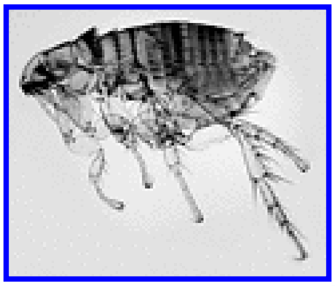
Information on the Internet

- Flea News
- Fleas Home Page of the Zoological Institute, St.Petersburg
- Checklist of South African Fleas

Title Illustrations



Scientific Name	Xenopsylla cheopis
Comments	Oriental rat flea. This flea is responsible for transmitting the bacterium Yersinia pestis, the causative agent of plague.
Acknowledgements	photo courtesy Public Health Image Library
Sex	Female
Life Cycle Stage	adult



Scientific Name Ctenocephalides felis
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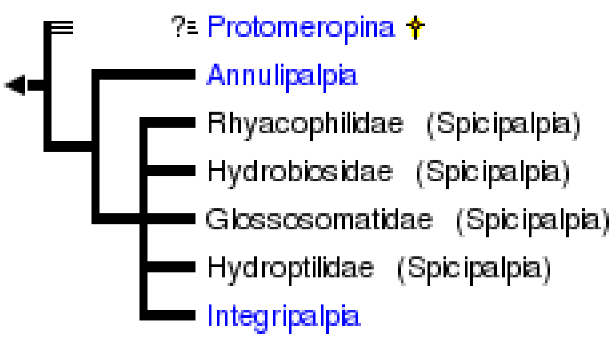
Trichoptera

Caddisflies

Ralph W. Holzenthal, Roger J. Blahnik, and Aysha Prather



Containing group: Endopterygota

Introduction

Trichoptera, or caddisflies, comprise the most diverse insect order whose members are exclusively aquatic. Only aquatic Diptera outnumber them in species and ecological diversity. The larval stages are found in lakes, rivers, and streams around the world, and are important components of food webs in these freshwater ecosystems (Resh and Rosenberg 1984). A few species in the family Chathamiidae from New Zealand and Australia are unusual for the Insecta in having larvae that are truly marine, mostly restricted to tidal pools.

Adult Trichoptera, in contrast to the larvae, are terrestrial and look much like drab, fragile moths, often occurring in large numbers in lakeside or streamside habitats. The similarity is not incidental. Trichoptera are closely related to the order Lepidoptera and together the two orders comprise the superorder Amphiesmenoptera, or "dressed-up wings," the name referring to the dense clothing of scales or hairs on the wings. Monophyly of these two orders is strongly supported in both morphological and molecular analyses (Kristensen 1984, Wheeler, et al. 2001). Trichoptera possess the more primitive character state, having hairs rather than scales, and this character accounts for the name Trichoptera, meaning "hairy wings." Also, unlike moths and butterflies, which typically have a coiled, tubelike proboscis for feeding, adult caddisflies lack well-developed mouthparts, including the absence of mandibles, but have a well-developed haustellum (synapomorphic for the order) formed from a fusion of the hypopharynx and labium, and used in some species to imbibe liquids.

Unlike Lepidoptera larvae, which are predominantly terrestrial herbivores, Trichoptera larvae, with very few exceptions, are aquatic and primarily detritivorous. Like lepidopteran caterpillars, caddisfly larvae are capable of spinning silk from specially modified salivary glands. The diversity of microhabitats exploited by caddisfly larvae is a consequence of the many ways silk is used to construct retreats, nets, and cases and probably accounts for the success of the order as a whole (Mackay and Wiggins 1979, Wiggins 1996).

Almost 12,000 caddisfly species, placed in 45 families and about 600 genera, have been described from all faunal regions, but it has been estimated that the world fauna may contain as many as 50,000 species (Schmid 1984). The three currently recognized suborders are largely characterized by differences in the way silk is used (Ross 1944), whether to produce nets or tubes, or as glue to make various types of portable cases, often incorporating sand and small pebbles, or bits of leaves and twigs, each genus or even species building its own particular style of case. Some larvae are free-living and predaceous, but nevertheless lay down a strand of silk as they move, much like the larvae of Lepidoptera.

The larvae, and the fascinating nets and cases they produce, represents the life stage most familiar to the non-entomologist, and the case-making behavior of some species may account for the English common name, caddisfly. Although the origin of the word is obscure, it has been suggested to derive from cadaz or cadace (caddys), a word of variable spelling used in

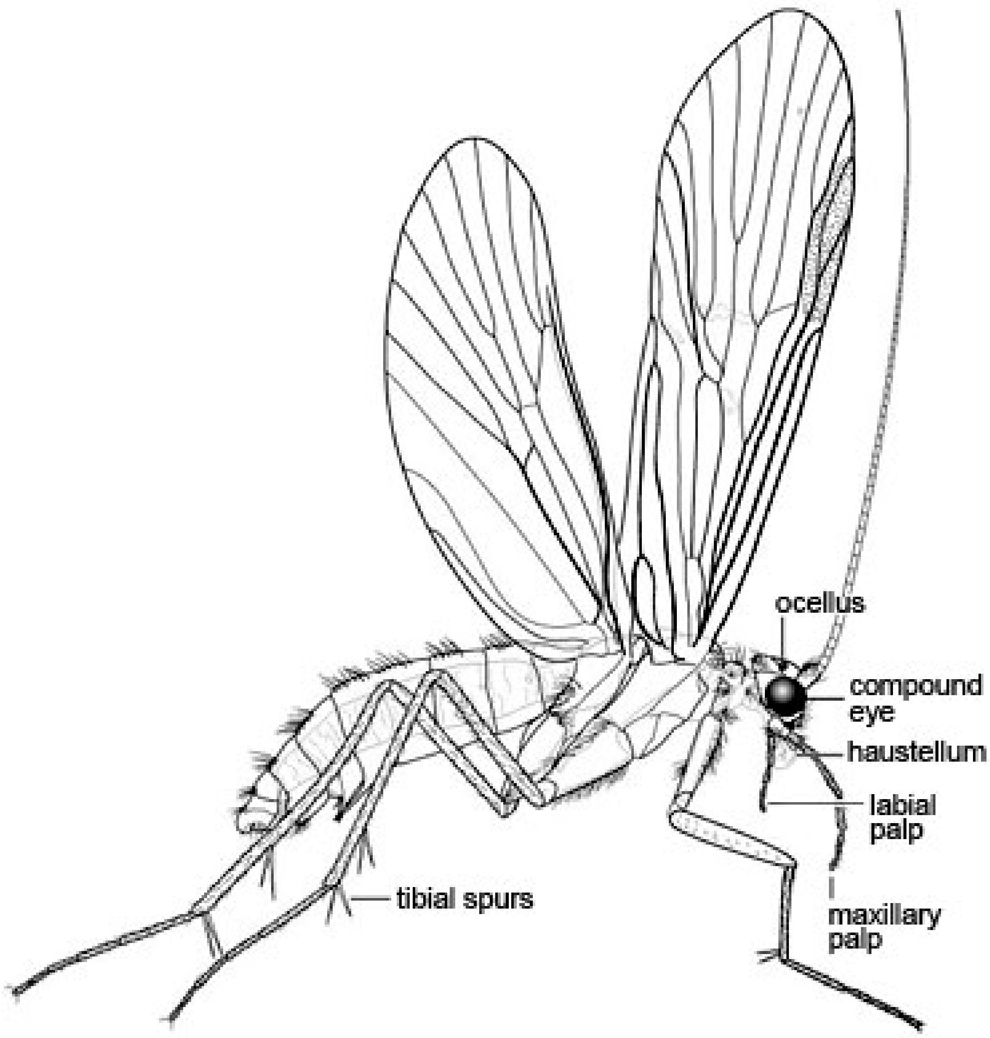
Shakespearean times to refer to a ribbon made from a certain kind of yarn sold by traveling vendors, who because of this were sometimes called "cadice men." Cadice men would pin samples of their wares to their clothing, a habit which may have suggested the name caddisfly or caddisworm for the aquatic larvae, who exhibit the analogous behavior of attaching bits of leaves and twigs to the outside of their cases (Hickin 1967).

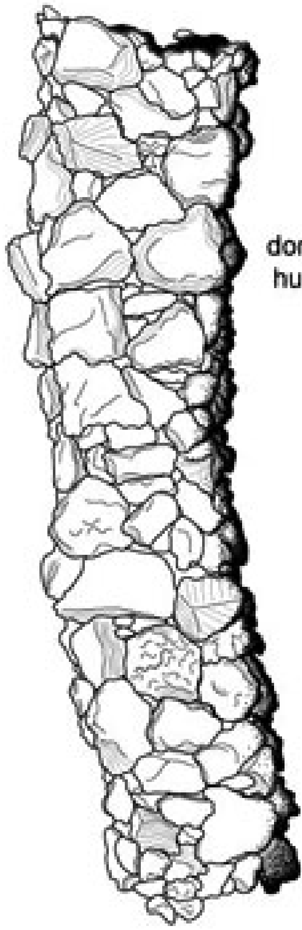
Although caddisflies are not generally considered to be of great economic importance as pests, they are beneficially important in the trophic dynamics and energy flow in aquatic ecosystems. The larvae are also useful as biological indicator organisms for assessing water quality. Extensive use of them has been made for this purpose because larvae of different species vary in sensitivity to various types of pollution (Resh and Unzicker 1975, Resh 1993, Dohet 2002), and because the taxonomy of the group is relatively well known for temperate regions. Unfortunately, the larvae of many species, especially in the tropics, are unknown or have not been associated with their adult forms.

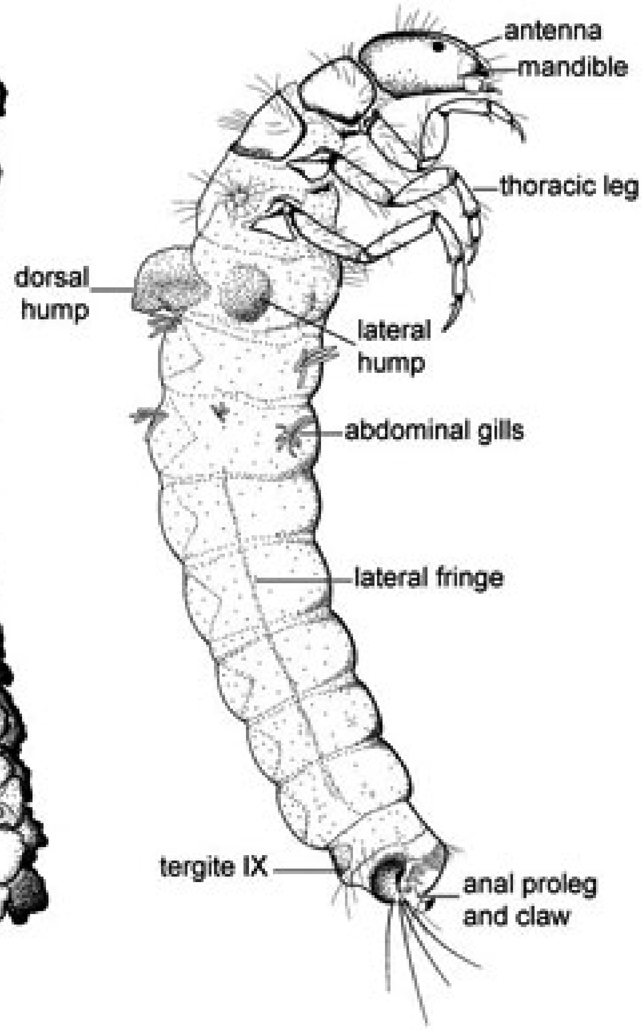
Characteristics

Caddisflies are easily recognized by a number of features. Adult mouthparts are reduced, with mandibles essentially absent, but the maxillary and labial palps, and often the haustellum, are prominent. The compound eyes are well developed, and ocelli may or may not be present. The forewings are somewhat longer than the hind wings, although the hind wings may be broader. Both pairs of wings and the body are usually covered with setae, or hairs, and occasionally with patches of scales. The wings are generally held rooflike when folded over the body. In most species the antennae are filamentous and about as long as the body, but in some families they can be several times longer than the body. Tibial spurs on the legs are conspicuous.

Larvae are aquatic and construct a case or retreat, except for a couple of "free-living" families. Like most holometabolous larvae, they have well developed mandibulate mouthparts and the thoracic legs are well developed, but abdominal prolegs are absent except for a pair of anal prolegs on the last abdominal segment, each proleg bearing a strong "anal claw." The exarate pupae are also aquatic, and have dectitious mandibles in most families.


ocellus
compound
eye
haustellum
labial
palp
maxillary
palp
tibial spurs





Caddisfly adult (Spicipalpia: Hydrobiosidae).
Illustration copyright © 2004, Lourdes Chamorro-Lacayo.

Caddisfly larva and case (Integripalpia: Odontoceridae).
Illustration copyright © 2004, Lourdes Chamorro-Lacayo.

The monophyly of the order Trichoptera is very well established. Following is a list of some characters that have been proposed as synapomorphic for the order (Weaver 1984, Kristensen 1991):

- Larvae aquatic, apneustic (no open spiracles), respiration epidermal, often by filamentous abdominal gills
- Larval tentorium reduced, delicate
- Larval antennae greatly reduced
- Larval abdominal segments I-IX without prolegs
- Larval abdominal segment IX with dorsal tergite
- Adult mandibles reduced, with loss of mandibular articulation
- Adult prelabium joined with hypopharynx to form a unique "haustellum" which serves as a lapping/sponging organ

Discussion of Phylogenetic Relationships

There has been considerable disagreement about the basal relationships of Trichoptera. This has resulted not only in different hypotheses about the evolutionary history of the group, but also in a confusion in the use of taxonomic categories, since different authors use different terminology, or have been inconsistent in how certain taxonomic categories have been used. In general, three major groups have been recognized, more or less corresponding to the different ecological adaptations of the larvae. We refer to these by their most common subordinal names, Annulipalpia, Spicipalpia, and Integripalpia (each in its most restricted sense and as used by Wiggins and Wichard 1989). However, the respective superordinal names of Hydropsychoidea, Rhyacophiloidea, and Limnephiloidea, respectively (sensu Ross 1956, Neboiss 1991), have sometimes been used to refer to groups of equivalent taxonomic coverage.

Because life history strategies have been used in constructing theories of caddisfly phylogenetic relationships, it is useful to review the life histories of the major groups:

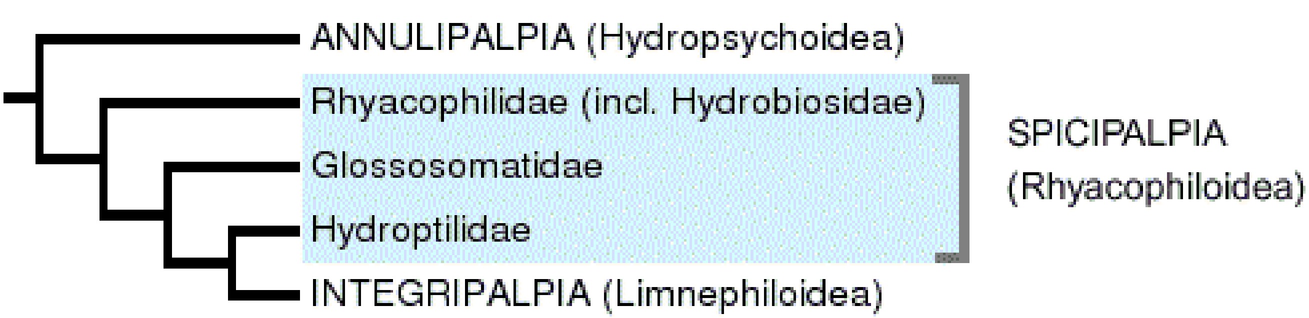
- The **Annulipalpia** includes all of the families whose larvae make retreats and capture nets.

- The **Spicipalpia** includes several rather different groups, each with different larval habits:
    1. free-living and predaceous (Rhyacophilidae and Hydrobiosidae) - build no larval structures, but pupate within a domelike enclosure of mineral fragments.
    2. purse-case makers (Hydroptilidae) - free-living until the last larval instar, and then construct a case which is portable or cemented to the substrate and in which the larvae eventually pupate.
    3. tortoise-case or saddle-case makers (Glossosomatidae) - make a case that is constructed very much like the pupal cases of Annulipalpia and the free-living Spicipalpia, consisting of a dome of small sand grains and pebbles. However (to complete the analogy to a tortoise) the larva also makes a transverse strap beneath the dome, allowing the larva to carry it on its back. The tortoise-case makers construct a new and bigger case with each larval instar, and then pupate within the last larval case, after removing the ventral strap and attaching the case to the substrate.

- The **Integripalpia** have been called the tube-case makers, because they most commonly construct a tubular case. The case, however, can be made from very different materials or formed in peculiar ways in various species. The larvae are mobile and simply extend or add to the case with each larval instar, eventually pupating inside the slightly modified larval case.

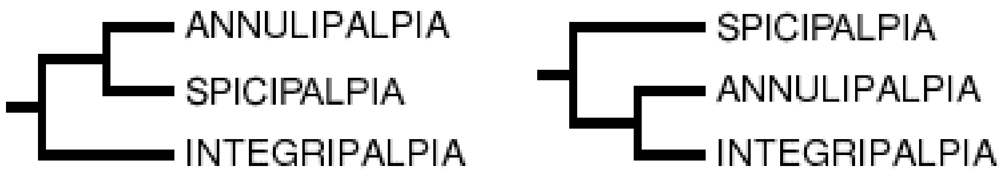
There is broad agreement about the monophyly of two of these major taxonomic groups, the Annulipalpia and Integripalpia (as defined above), and considerable disagreement about the monophyly and relative placement of taxa within the Spicipalpia.

Morse (1997) provided a thorough summary of the hypotheses of relationships proposed for the major groups of Trichoptera and also of the status of phylogenetic work at the family and genus level undertaken to date. Ross (1956) was the first to identify explicitly any derived characters for caddisfly taxa. He recognized two monophyletic suborders, Annulipalpia (equivalent to his superfamily Hydropsychoidea) and Integripalpia. These subordinal names were first established by Martynov (1924). Ross's Integripalpia contained two superfamilies, Rhyacophiloidea and Limnephiloidea. These superfamilies are equivalent to the suborders Spicipalpia and Integripalpia, as used here. However, Ross's Rhyacophiloidea (Spicipalpia) was paraphyletic as originally defined. Further, his hypothesis of the relationships among the three rhyacophiloid families (Rhyacophilidae [including Hydrobiosidae], Glossosomatidae, and Hydroptilidae) and the Limnephiloidea was based mainly on a presumed evolutionary transformation in larval case/pupal cocoon making behavior. Ross lacked morphological synapomorphies at his Glossosomatidae + Hydroptilidae + Limnephiloidea node and had only one at his Hydroptilidae + Limnephiloidea node. Thus his behavioral transformation series is supported by only one non-behavioral character.



Ross (1956, 1964, 1967)

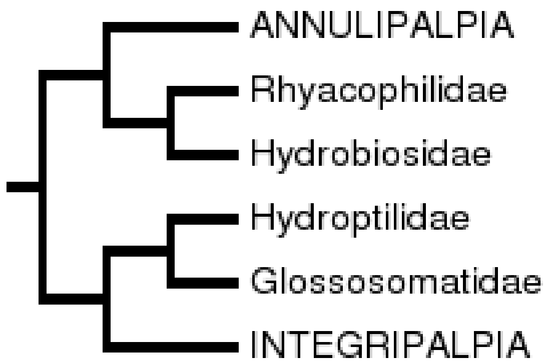
Weaver (1983, 1984, 1992a,b; also Weaver & Morse, 1986) was the first to apply cladistic principles to caddisfly higher level classification and examined about twice as many morphological characters as Ross. Weaver (1984) concluded that Spicipalpia (which he treated as an infraorder within a more broadly defined suborder Annulipalpia) was monophyletic and had a sister taxon relationship to the infraorder Curvipalpia (= Annulipalpia of Ross and as used here). Weaver restricted his concept of Integripalpia to include only the Limnephiloidea of Ross, and this is the sense in which it is used here.



Weaver (1984)   Wiggins and Wichard (1989)

Later, Wiggins and Wichard (1989; also Wiggins 1992, Wichard 1991, Wichard et al. 1993, Wichard et al. 1997) proposed a sister group relationship between Annulipalpia and Integripalpia, based on an interpretation of pupal cocoon evolution in Trichoptera. Their phylogeny is based on the hypothesis that the closed, semipermeable cocoons of parchmentlike silk found in the spicipalpian families represent the groundplan condition of the order, and the cocoons of permeable silk with ventilation openings found in the Annulipalpia and Integripalpia are derived. A more detailed account of behavioral evolution in Trichoptera is found in the treatise of Frania and Wiggins (1997), who hypothesized that the ancestral habitat for the order Trichoptera was in cool, flowing, well-oxygenated water. This can be contrasted with the theory of Weaver and Morse (1986), who proposed that the ancestral trichopteran habitat was in subterranean silk-lined tubes in saturated soil. However, Kristensen (1997), pointed out that silk-lined tubes in Lepidoptera do not appear until the eight branch from the base of the tree, in Neolepidoptera (Exoporia), and thus this adaptation cannot be assumed to be ancestral within Trichoptera. Based on their hypothesis of evolution in the group, Wiggins, Wichard, and Frania would elevate Weaver's Infraorder Spicipalpia to a third suborder, coordinate with Annulipalpia and Integripalpia. According to Wiggins (1992), the pupation hypothesis was not intended as a statement of higher level trichopteran relationships; the recognition of Spicipalpia was one of convenience, since it serves to focus discussion on the unresolved problem of basal relationships in Trichoptera. These workers preferred to consider the relationships of the three suborders as currently unresolved.

In the study by Frania and Wiggins (1997), the hypothesis of a basal Spicipalpia was tested using a computer assisted parsimony analysis of 70 morphological larval and adult characters, which included the majority of families in the order. Characters were polarized using a hypothetical caddisfly ancestor, whose character states were inferred through consideration of character states in Mecoptera and Lepidoptera. The results could be considered equivocal at best, since they do not support either monophyly of Spicipalpia or of a basal position of Spicipalpia. The strict consensus phylogeny most closely resembles the hypothesis of Ivanov (1997, 2002):



Ivanov (1997, 2002)

Ivanov proposed that Hydroptilidae and Glossosomatidae of the Spicipalpia are sister taxa and allied to the Integripalpia, and that Rhyacophilidae and Hydrobiosidae are sister taxa allied to the Annulipalpia. He specifically challenged Weaver's hypothesis of spicipalpian monophyly, providing evidence that each of Weaver's 4 spicipalpian apomorphies are plesiomorphic. Frania and Wiggins similarly found Hydroptilidae to be closely related to Integripalpia, but the relationship of Glossosomatidae was less certain, depending on the analysis performed. Using selected characters they suggested that Glossosomatidae might be allied to Hydrobiosidae and Rhyacophilidae and basal to Annulipalpia, but were uncertain about the relationship of Hydroptilidae. In the cladograms presented, it was sister taxon to the Integripalpia, suggesting that Spicipalpia may not be monophyletic.

The most recent and complete analysis of basal relationships in Trichoptera is that of Kjer et al. (2001, 2002), who used a molecular dataset of several gene fragments, including mitochondrial, and nuclear DNA, and also included the morphological characters of Frania and Wiggins. Forty-three of forty-five families were included, and both parsimony and likelihood analyses were performed. This combined data analysis is the hypothesis of relationships presented above. In Kjer et al.'s analysis, Annulipalpia and Integripalpia were monophyletic and Spicipalpia was paraphyletically arranged at the base of the Integripalpia, as in Ross's hypothesis. The relationship of spicipalpians to Integripalpia was strongly supported, and Kjer et al. (2001, 2002) rejected the separation of some families of spicipalpians with Annulipalpia, as in the Ivanov (1997, 2002) and Frania and Wiggins (1997) morphology-based hypotheses. In fact, a differentially weighted analysis performed in Kjer et al. (2001) of the Frania and Wiggins (1997) morphological data recovered a phylogenetic hypothesis that was identical to Ross (1967). However, paraphyly of Spicipalpia was only weakly supported and the possibility that Spicipalpia is monophyletic could not be eliminated. Some partitions of the data supported a monophyletic Spicipalpia, and by most analytical criteria, a monophyletic Spicipalpia was only slightly suboptimal.

Determining the relative relationships among the families of Spicipalpia remains the next challenging question in resolving basal relationships in Trichoptera and in helping to resolve the question of the evolution of net and case-making behavior in the order.

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- World Trichoptera Checklist, Dr. John C. Morse (editor), Clemson University

- Orden Trichoptera, INBio, Insect Families of Costa Rica (in Spanish)

- TRICH-L, the Trichoptera discussion group list. To subscribe send the following message IN THE BODY ONLY:
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  to the following address:
  cuentsubscribe@entoinfo.clemson.edu

Title Illustrations

- Nectopsyche utleyorum Holzenthal 1996 (Integripalpia: Leptoceridae), Guanacaste, Costa Rica. Illustration copyright © 1997, David Funk.
- Grumichella sp. (Integripalpia: Leptoceridae), Río Montalban, Venezuela. Illustration copyright © 1997, James C. Hodges, Jr.

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About This Page

Ralph W. Holzenthal
holze001@umn.edu
Department of Entomology
219 Hodson Hall
1980 Folwell Ave.
University of Minnesota
St. Paul, Minnesota 55108
USA

Roger J. Blahnik

blahn003@umn.edu
Department of Entomology
219 Hodson Hall
1980 Folwell Ave.
University of Minnesota
St. Paul, Minnesota 55108
USA

Aysha Prather
prat0058@umn.edu
Centre for Biodiversity and Conservation Biology
Royal Ontario Museum
100 Queen's Park
Toronto Ontario M5S 2C6
Canada

Correspondence regarding this page should be directed to Roger J. Blahnik at blahn003@umn.edu

- First online 14 February 1997

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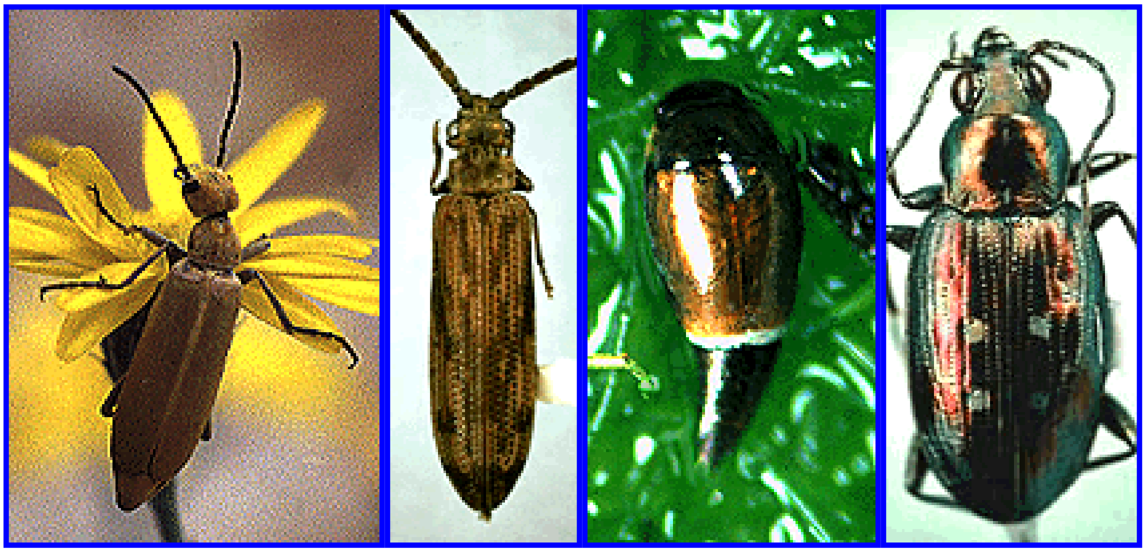
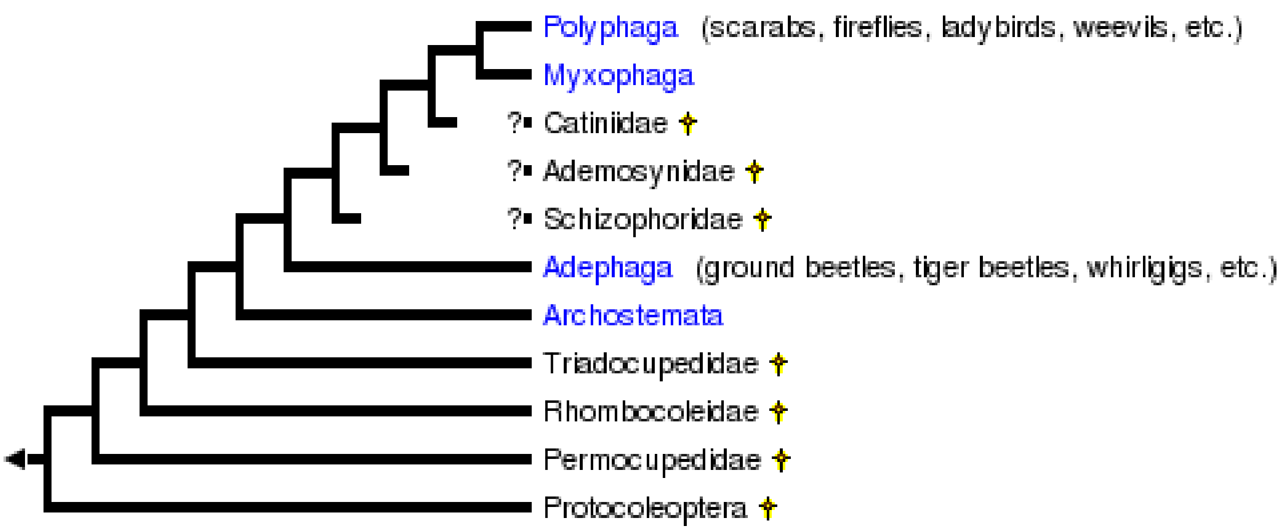
Coleoptera

Beetles

David R. Maddison





Tree from Beutel (1997) and Beutel and Haas (2000).
Containing group: Endopterygota

Introduction

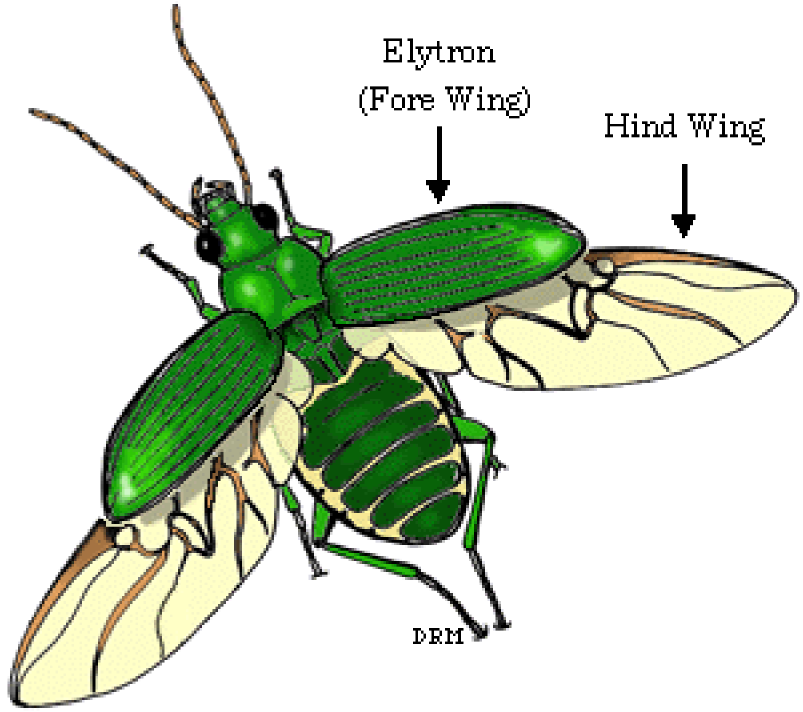
The Coleoptera, or beetles, includes many commonly encountered insects such as ladybird beetles (family Coccinellidae), click beetles (Elateridae), scarabs (Scarabaeidae), and fireflies (Lampyridae). They live throughout the world (except Antarctica), but are most speciose in the tropics.

The oldest beetle fossils are from the Lower Permian (about 265 million years old; Ponomarenko, 1995); since then the group has diversified into many different forms. They range in size from minute featherwing beetles (Ptiliidae), adults of which are as small as 0.3 mm long, to the giant Goliath and Hercules beetles (Scarabaeidae), which can be well over 15 cm. While most species are phytophagous, many are predacious, or fungivores, or are parasitoids. They communicate to one another in many ways, either by use of chemicals (e.g. pheromones), sounds (e.g. stridulation), or by visual means (e.g. fireflies). They live in rainforest canopies, the driest deserts, in lakes, and above treeline on mountains.

In one sense the most unusual property of beetles is not some aspect of their structure or natural history, but their sheer number. There are more known species of Coleoptera than any other group of organisms, with over 350,000 described species. Perhaps the most famous quote about beetles comes from the great population geneticist J.B.S. Haldane, who was asked what might be learned about a Creator by examining the world. His response: "an inordinate fondness for beetles" (Fisher, 1988).

Characteristics

The most distinctive feature of beetles is the hardening of the forewings into elytra; it is from this that they get their formal name (koleos - sheath, pteron - wing). The elytra serve to protect the more delicate hind wings, as well as the dorsal surface of the abdomen, and may have been a key factor allowing them to exploit narrow passageways (for example, in leaf litter and under bark). During flight the forewings are opened enough to allow the hind wings to unfold and function:



Other derived characteristics of beetles are:

- hind wings folded under elytra, with reduced venation
- hind two thoracic segments (mesothorax+metathorax=pterothorax) broadly connected with abdomen, so that the primary functional units of body are head / prothorax / pterothorax + abdomen, rather than the more typical head / thorax / abdomen of many other insects.
- genitalia retracted into abdomen
- adult antenna with 11 articles

Beetles are holometabolous insects, normally with adecticous, exarate pupae. Most species have chewing mouthparts. There is a gula present on the undersurface of the head.

The Suborders of Coleoptera

The four living suborders of beetles diverged from one another in the Permian and early Triassic, and are substantially different from one another. Adults differ in the structure of the prothorax, hind wing, abdomen, ovary, testes, and so on. The major differences are summarized in a table.

Polyphaga is by far the largest suborder, containing 85% of the known species, including rove beetles, scarabs, stag beetles, metallic wood-boring beetles, click beetles, fireflies, blister beetles, mealworms, ladybirds, leaf beetles, longhorn beetles, and weevils. Many are phytophagous. Adephaga includes ground beetles, tiger beetles, predacious diving beetles, and whirligig beetles; most adephagans are predacious. Myxophaga is a small suborder, containing less than 100 known species, whose members are small or minute, and associated with hygropetric habitats, drift material, or interstitial habitats among sand grains. Archostemata contains several families of beetles, most associated with wood; members of this family are somewhat similar to some of the earliest, Paleozoic beetle fossils.

Discussion of Phylogenetic Relationships

Compared to the other four large orders of insects (Hemiptera, Hymenoptera, Diptera, and Lepidoptera), the phylogenetic relationships of the major lineages of beetles are relatively poorly known. Only recently has some of the morphological data been examined phylogenetically (e.g., Beutel, 1997; Beutel and Haas, 2000), and molecular sequence information is only now being gathered.

There are several competing hypotheses regarding subordinal relationships. The two most widely discussed differ most strikingly in their placement of the suborder Polyphaga: this suborder is either the sister group of Myxophaga (Crowson, 1960, 1981; Machatschke, 1962; Klausnitzer, 1975; Beutel, 1997; Beutel and Haas, 2000), or the sister group of all remaining beetles (Lawrence and Newton, 1982; Kukalová-Peck and Lawrence, 1993), as shown in the following two figures:

```
     ========= Archostemata                ========= Polyphaga
     |                                     |
     |  ====== Adephaga                    |  ====== Archostemata
 ====|  |                              ====|  |
     ===|  === Myxophaga                   ===|  === Myxophaga
        ===|                                  ===|
           === Polyphaga                         === Adephaga

"Polyphaga+Myxophaga" hypothesis     "Basal Polyphaga" hypothesis
```

Evidence for a close relationship of Polyphaga to Myxophaga includes the shared reduction in the number of larval leg articles (Crowson, 1960, 1981). Klausnitzer (1975) further considered the Adephaga as sister to Myxophaga + Polyphaga, based on completely sclerotized elytra, reduced number of crossveins in the hind wings, and folded (as opposed to rolled) hind wings of those three suborders.

Evidence for the alternative hypothesis, that Polyphaga is the sister group to remaining beetles, is based primarily on characters of wing structure, and on the loss of the cervical sclerites in the three suborders other than Polyphaga (Lawrence and Newton, 1982; Kukalová-Peck and Lawrence, 1993).

Recent cladistic analyses of some of the morphological data (Beutel, 1997; Beutel and Haas, 2000) supports the Polyphaga + Myxophaga hypothesis.

The composition of the clade Coleoptera is not in dispute, with the exception of the twisted-wing parasites, Strepsiptera. These odd insects have been regarded as related to the beetle families Rhipiphoridae and Meloidae, with which they share first instar larvae that are active, host-seeking triungulins and later instar larvae that are endoparasites of other insects (Crowson, 1981), or as the sister group of beetles (e.g. Kukulová-Peck and Lawrence, 1993), or more distantly related to insects (see further discussion in Strepsiptera).

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- Water Beetle World. The newsletter for aquatic Coleoptera workers.
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- Los Lamelicornios de Costa Rica.
- A Distributional Checklist of the Beetles (Coleoptera) of Florida.
- Coleoptera of Rhode Island: An on-line database.
- The Beetles of the Virgin Islands.
- The Quaternary Entomology Laboratory at the University of Waterloo. Provides an introduction to fossil beetle studies.
- Shapes and Colors from the World of Beetles. Thais Entomology.
- An Inordinate Fondness for Beetles (A. V. Evans & C. L. Bellamy).
- Beetle Breeding Web.
- Beetles (Coleoptera) and Coleopterists

Title Illustrations

From left to right:

- Blister beetle (Meloidae, Polyphaga). U.S.A.: Arizona.
- *Tenomerga concolor* (Cupedidae, Archostemata). Canada: Ontario: Burlington.
- *Hydroscapha natans* (Hydroscaphidae, Myxophaga). U.S.A.: Arizona: Sycamore Canyon.
- *Bembidion inaequale* (Carabidae, Adephaga). Canada: Alberta: Gull Lake.

Scientific Name	Meloidae
Location	U.S.A.: Arizona
Comments	Blister beetle (Polyphaga) on a composite flower
Specimen Condition	Live Specimen
Copyright	© 1995 David R. Maddison

Scientific Name	Tenomerga concolor
Location	Canada: Ontario: Burlington
Copyright	© 1995 David R. Maddison

Scientific Name	Hydroscapha natans
Location	U.S.A.: Arizona: Sycamore Canyon
Copyright	© 1995 David R. Maddison

Scientific Name	Bembidion inaequale
Location	Canada: Alberta: Gull Lake
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About This Page

David R. Maddison
beetle@ag.arizona.edu
Department of Entomology
University of Arizona
Tucson, AZ 85721

- First online 16 November 1994
- Content changed 11 September 2000

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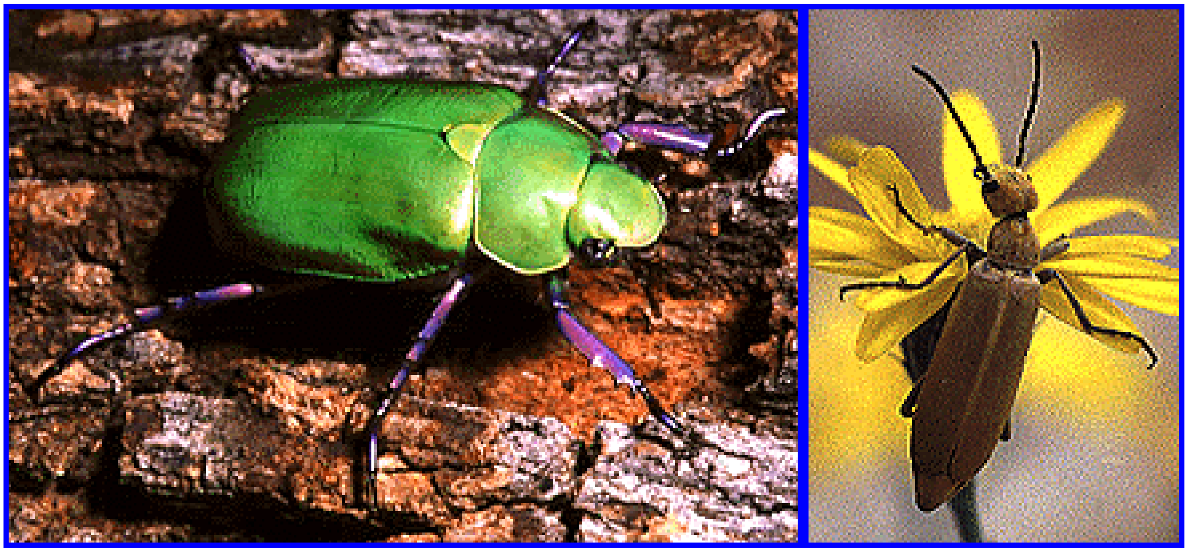
Polyphaga



Tree partly from Kukalová-Peck and Lawrence (1993).
Containing group: Coleoptera

Introduction

The suborder Polyphaga contains the majority of beetles, with about 300,000 described species.

Among the commonly encountered polyphagans are the rove beetles (Staphylinoidea), scarabs and stag beetles (Scarabaeoidea), metallic wood-boring beetles (Buprestoidea), click beetles and fireflies (Elateroidea), as well as fungus beetles, grain beetles, ladybird beetles, darkling beetles, blister beetles, longhorn beetles, leaf beetles, and weevils (all Cucujiformia).

Aquatic lineages have evolved several times within Polyphaga. The largest groups are found within Hydrophiloidea and Byrrhoidea.

Characteristics

Polyphagan beetles do not have the pleuron of the prothorax externally visible; instead, remnants of the propleuron are present internally as a "cryptopleuron" (Hlavac 1972, 1975; Lawrence and Newton, 1982). Because the lack of the pleuron in the external body wall, at most one suture (that between the notum and the sternum) is visible in the prothorax in polyphagans. In members of other suborders, two sutures (the sternopleural and notopleural) are often externally visible (unless secondary fusion between the sclerites obfuscates the sutures, as in the case of Micromalthus).

Female polyphagan beetles have telotrophic ovarioles, a derived condition within beetles.

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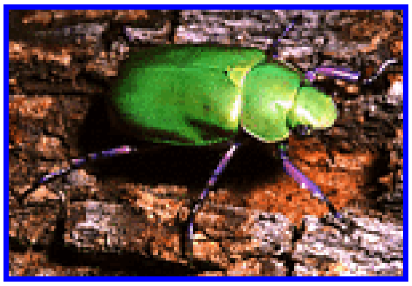
Pakaluk, J. and S.A. Slipinski (eds.) 1995. Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warszawa.

Information on the Internet

- Staphyliniformia
- Nicrophorus Central
- The Firefly Files
- Guide to Palearctic Flea Beetle Genera (Coleoptera: Chrysomelidae: Alticinae)

Title Illustrations



Scientific Name	Plusiotus beyeri
Location	Arizona
Copyright	© 1995 Cecil Schwalbe

Scientific Name	Meloidae
Location	U.S.A.: Arizona
Comments	Blister beetle (Polyphaga) on a composite flower
Specimen Condition	Live Specimen
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Correspondence regarding this page should be directed to David R. Maddison at beetle@ag.arizona.edu

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Myxophaga

Tree from Beutel, Maddison, and Haas (1999) and Beutel (1999).

Containing group: Coleoptera

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Title Illustrations

Scientific Name	Sphaerius sp.
Location	USA: Arizona: Sycamore Canyon
Specimen Condition	Live Specimen
Life Cycle Stage	adult
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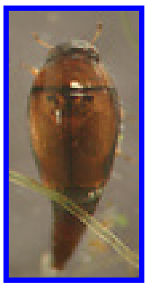

Scientific Name	Hydroscapha natans
Location	USA: Arizona: Sycamore Canyon
Specimen Condition	Live Specimen
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  - Gyrinidae
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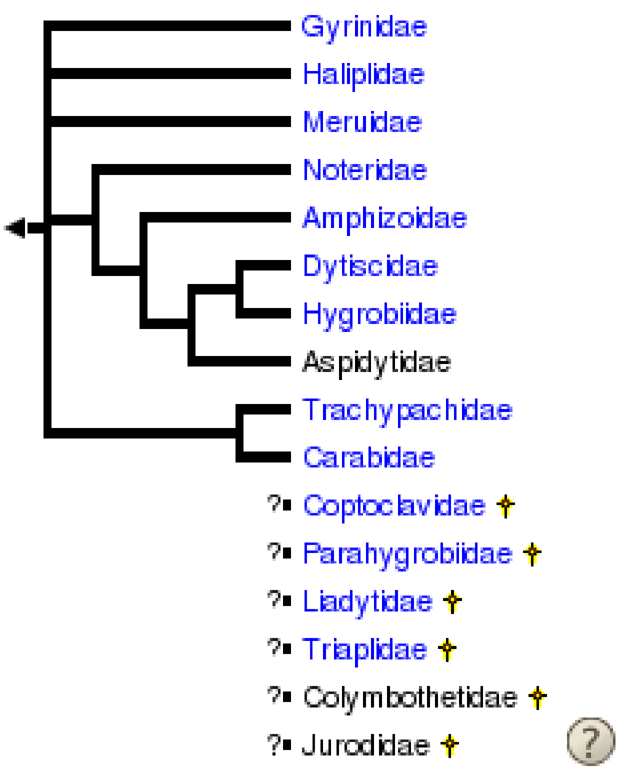
  - Liadytes
  - Meruidae

- Noteridae
- Parahygrobia natans
- Trachypachidae
- Triaplidae

Adephaga

Ground beetles, tiger beetles, whirligigs, predacious diving beetles, wrinkled bark beetles, and others

David R. Maddison



Two clades often considered as separate families, the tiger beetles and wrinkled bark beetles, are here treated as subgroups of the family Carabidae (as the supertribe

Cicindelitae and the tribe Rhysodini, respectively)
Containing group: Coleoptera

Introduction

The Adephaga is the second largest suborder of beetles, with over 40,000 known species. Most members are predacious (the Greek word "adephagos" means "gluttonous"). The two living families with terrestrial members, Carabidae and Trachypachidae, are occasionally called the Geadephaga; the remaining, aquatic families are the Hydradephaga. The majority of species in the suborder belong to the family Carabidae.

Adephagans diverged from their sister group in the late Permian, with the most recent common ancestor of living adephagans probably existing in the early Triassic, around 240 million years ago (Ponomarenko, 1977; Erwin, 1979). Both aquatic and terrestrial representatives of the suborder appear in the fossil record in the late Triassic, with a Jurassic fauna consisting of trachypachid, carabid, gyrinid, and haliplid-like forms (Ponomarenko, 1977). The familial and tribal diversification of the group spans the Mesozoic period, with a few tribes radiating explosively in the Tertiary (e.g., members of the carabid subfamily Harpalinae, Erwin, 1985).

Adephagans are diverse in diet and structure. Most are general predators, although algal feeders (Haliplidae), seed feeders (many harpaline carabids), fungal feeders (rhysodines), specialist predators on snails (licinine and cychrine carabids), and ectoparasitoids of other insects (brachinine and lebiine carabids) or millipedes (peleciine carabids), occur. Many lineages have gone down, into caves, while others have gone up, into the rain forest canopy or alpine habitats. The body forms of some have become highly modified structurally for life in unusual habitats (e.g., gyrinids at the air-water interface, paussine carabids in ants' nests, rhysodines in heartwood). Some are ovoviparous (pseudomorphine carabids, Liebherr and Kavanaugh, 1985). A variety of chemical defense mechanisms have evolved in the group, including the explosive discharge of bombardier beetles (Aneschansley et al., 1969).

Characteristics

Members of the suborder have the following properties: Adults with notopleural sutures visible on prothorax, with six visible abdominal sterna, the first three fused and divided by hind coxae; pygidial defense glands; testes tubular, coiled, consisting of a single follicle; ovaries polytrophic. Larvae with fused labrum and no mandibular molae.

Discussion of Phylogenetic Relationships

Family-level relationships within Adephagans have been extensively examined, but no consensus has been reached (for some recent reviews, see Kavanaugh, 1986; Beutel, 1993). There has been detailed examination of head structure (Beutel, 1986, 1989a), thoracic sclerites and musculature (e.g., Bell, 1964, 1966, 1967, 1982; Nichols, 1985; Kavanaugh, 1986; Beutel, 1986, 1988, 1989b, 1990, 1992b) , female abdominal structure (Bils, 1976; Burmeister, 1976, 1980, 1990a, 1990b), ventral nerve cord (Heath and Evans, 1990), digestive system (Yahiro, 1990), wing venation (Ward, 1979), larvae (e.g., Liebherr and Ball, 1990; Bousquet and Smetana, 1991; Beutel, 1991a, 1991b, 1992a, 1992c, 1993; Arndt, 1993), chromosomes (Serrano, 1981b; Serrano and Yadav, 1984), defensive glands (Forsyth, 1972; Kanehisa and Murase, 1977), and defensive secretions (e.g., Kanehisa and Murase, 1977; Moore, 1979; Kanehisa and Kawazu, 1985).

The following three phylogenetic hypotheses give an indication of the controversies surrounding the phylogeny of adephagans. This first tree is from Baehr (1979):

```
                 ========= Amphizoidae
                 |
                 |  ====== Hygrobidae
              ===|  |
           ===|  ===|  === Haliplidae
        ===|  |     ===|
     ===|  |  |        === Noteridae
=====|  |  |  |
     |  |  |  ============ Dytiscidae
     |  |  |
     |  |  =============== Gyrinidae
     |  |
     |  ================== Trachypachidae
     |
     ===================== Carabidae
```

this second from Kavanaugh (1986):

```
              === Gyrinidae
           ===|
           |  === Hygrobidae
        ===|
```

```
     ===|  |  === Noteridae
        |  |  ===|
        |  |     === Dytiscidae
=====|  |
        |  ========= Amphizoidae
        |
        |  ========= Haliplidae
        |  |
     ===|  ====== Trachypachidae
        ===|
           ====== Carabidae
```

and this tree from Beutel (1995):

```
     ==================== Gyrinidae
     |
     |  ================== Haliplidae
     |  |
     |  |     ============ Trachypachidae
     |  |     |
     |  |     |  ========= Noteridae
     |  |     |  |
=====|  |  ===|  |  ====== Amphizoidae
     ===|  |  ===|  |
        ===|     ===|  === Hygrobidae
           |        ===|
           |           === Dytiscidae
           |
           | ============= Rhysodini
           ==|
             ============= Carabidae
```

Much of the attention has focused on a few controversial groups:

1. **Trachypachidae**: These are considered as either the sister group of Carabidae (e.g., Kavanaugh, 1986), or as the sister group to all or part of Hydradephaga (Bell, 1966; Hammond, 1979; Ward, 1979; Roughley, 1981; Evans, 1982; Arndt, 1993; Deuve, 1993). Bell (1982) believes that "understanding Trachypachus is the key to understanding the Adephaga." Superficially, these terrestrial beetles are very much like carabids, and have frequently been placed in the same family (Lindroth, 1961). However, trachypachids have glabrous antennae, immobilized hind coxae, and medial binding patches on their wings, and in this way are like dytiscimorph water beetles. If the adephagan ancestor was

aquatic or semi-aquatic, then trachypachids may represent an intermediate stage, with several morphological remnants (e.g., glabrous antennae) of an aquatic life (Kavanaugh, 1986; Ponomarenko, 1977). According to this view, later lineages lost other indications of an aquatic ancestry, and diversified into modern carabids. In contrast, if the adephagan ancestor was terrestrial, then features linking trachypachids and dytiscimorphs are derived, indicating a close relationship (Roughley, 1981; Bell, 1982).

2. **Omophronini**: This tribe is generally thought to be within Carabidae (many authors including Baehr, 1979; Beutel, 1993; Erwin, 1985), but has been proposed to be related to Hydradephaga and trachypachids (Nichols, 1985; Ruhnau, 1986; Deuve, 1993).
3. **Cicindelitae** (tiger beetles, here included within Carabidae): These may be a separate clade from carabids (Bils, 1976; Regenfuss, 1975), or they may belong within Carabidae, related to carabines (Deuve, 1993; Kavanaugh pers. comm.), hiletines (Ward, 1979), or loricerines (Arndt, 1993).
4. **Rhysodini**: Wrinkled bark beetles may be highly derived carabids, related to scaritines (Bell, 1967; Forsyth, 1972; Beutel, 1990, 1992a) or psydrites (Erwin, 1985) or they may lie outside of carabids (Arndt, 1993; Deuve, 1988; Beutel, 1993). In the Tree of Life project they are placed within carabids.

The critical questions about phylogeny of adephagan families revolve around the placement of the root of the adephagan clade, and the nature of the ancestor. Was the ancestral adephagan aquatic or terrestrial? Is the root next to Gyrinidae (Beutel and Roughley, 1994)? Is the root within terrestrial carabids, with hydradephagans arising within Carabidae (Bils, 1976; Nichols, 1985)? The long independent history of the other suborders of beetles has obscured morphological clues, making the information from outgroups suspect, and the position of the root questionable. For example, the possible sister group to the adephagans, the suborder Myxophaga (Kukalová-Peck and Lawrence, 1993), consists of minute or small aquatic (hygropetric) or interstitial beetles. The reduction in size and specialized habitat of these beetles might be associated with enough correlated, derived modifications to cast doubt upon use of their structural features in outgroup analysis. Hopefully the molecular sequence data currently being gathered will help clarify these issues.

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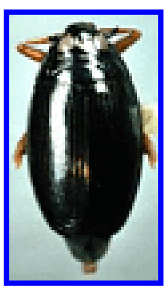
Title Illustrations

From left to right:

- Gyrinus sp. (family Gyrinidae), British Columbia, Canada.
- Haliplus fasciatus Aubé (family Haliplidae), North Carolina, U.S.A.
- Copelatus sulcatus Sharp (family Dytiscidae), Suriname.
- Bembidion lapponicum (family Carabidae), Saskatchewan, Canada.



Scientific Name	Gyrinus
Location	British Columbia, Canada
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Scientific Name	Haliplus fasciatus

Location	North Carolina, U.S.A.
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Scientific Name	Copelatus sulcatus
Location	Suriname
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Scientific Name	Bembidion lapponicum
Location	Saskatchewan, Canada
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About This Page

David R. Maddison
beetle@ag.arizona.edu
Department of Entomology
University of Arizona
Tucson, AZ 85721

Correspondence regarding this page should be directed to David R. Maddison at beetle@ag.arizona.edu

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Archostemata

Containing group: Coleoptera

Discussion of Phylogenetic Relationships

No phylogenetic analysis of this suborder is available.

Title Illustrations

Scientific Name	Omma stanleyi (Ommatidae)
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Scientific Name Rhipsideigma raffrayi (Cupedidae)

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Scientific Name Micromalthus debilis (Micromalthidae)

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  - Diptera
  - Hymenoptera
  - Lepidoptera
  - Mecoptera
  - Megaloptera
  - Miomoptera
  - Neuroptera
  - Raphidioptera
  - Siphonaptera
  - Strepsiptera
  - Trichoptera
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  - Subgroups
  - Bibionomorpha
  - Blephariceromorpha
  - Brachycera
  - Culicomorpha
  - Psychodomorpha (in part)
  - Ptychopteromorpha

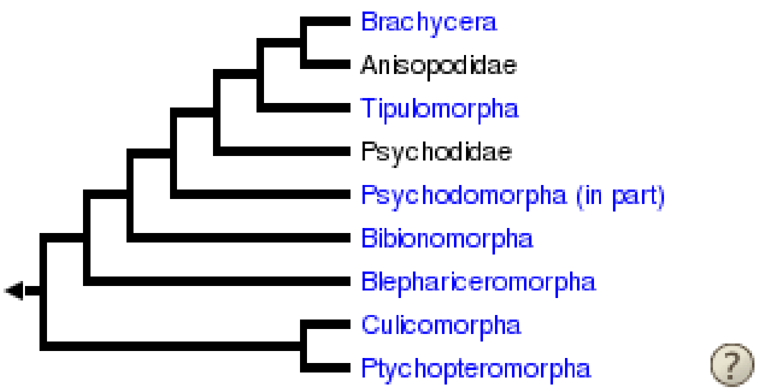
- [Tipulomorpha](#)

Diptera

True Flies

[Brian M. Wiegmann and David K. Yeates](#)





Tree from Oosterbroek and Courtney 1995; for a review of phylogenetic research on Diptera see Yeates and Wiegmann 1999 and Yeates et al. 2003.

Containing group: [Endopterygota](#)

Introduction

The Diptera are commonly known as (true) flies and include many familiar insects such as mosquitoes, black flies, midges, fruit flies, blow flies and house flies. Flies are generally common and can be found all over the world except Antarctica. Many species are particularly important as vectors of disease in man, other animals, and plants. In addition, much of our knowledge of animal genetics and development has been acquired using the vinegar fly [Drosophila melanogaster](#) (family Drosophilidae) as an experimental subject (Lawrence, 1992).

The earliest fossil flies are known from the Upper Triassic of the Mesozoic geological period, some 225 million years ago (Evenhuis, 1995).• Since that time they have diversified to become one of the largest groups of organisms. There have been about

120,000 species of flies formally described by scientists; thus about 1 in every 10 animals described is a fly. An equal number of species may await description and most of these will be found in environments that remain to be studied intensively, such as tropical forests.

Flies are holometabolous insects, that is their life cycle involes a major change in form from a soft-bodied, wingless larval stage to a hardened, winged adult.

Larval flies have a variety of common names, such as wriggler and maggot. Fly larvae have an enormous variety of feeding habits, and individual species often have very precise requirements. Many consume decaying organic matter, or are predacious, and a large proportion are parasitic on other insects and other organisms. Adult flies are almost always free-living and fly during the day. They typically consume liquid food such as nectar and other plant exudates, or often decomposing organic matter.

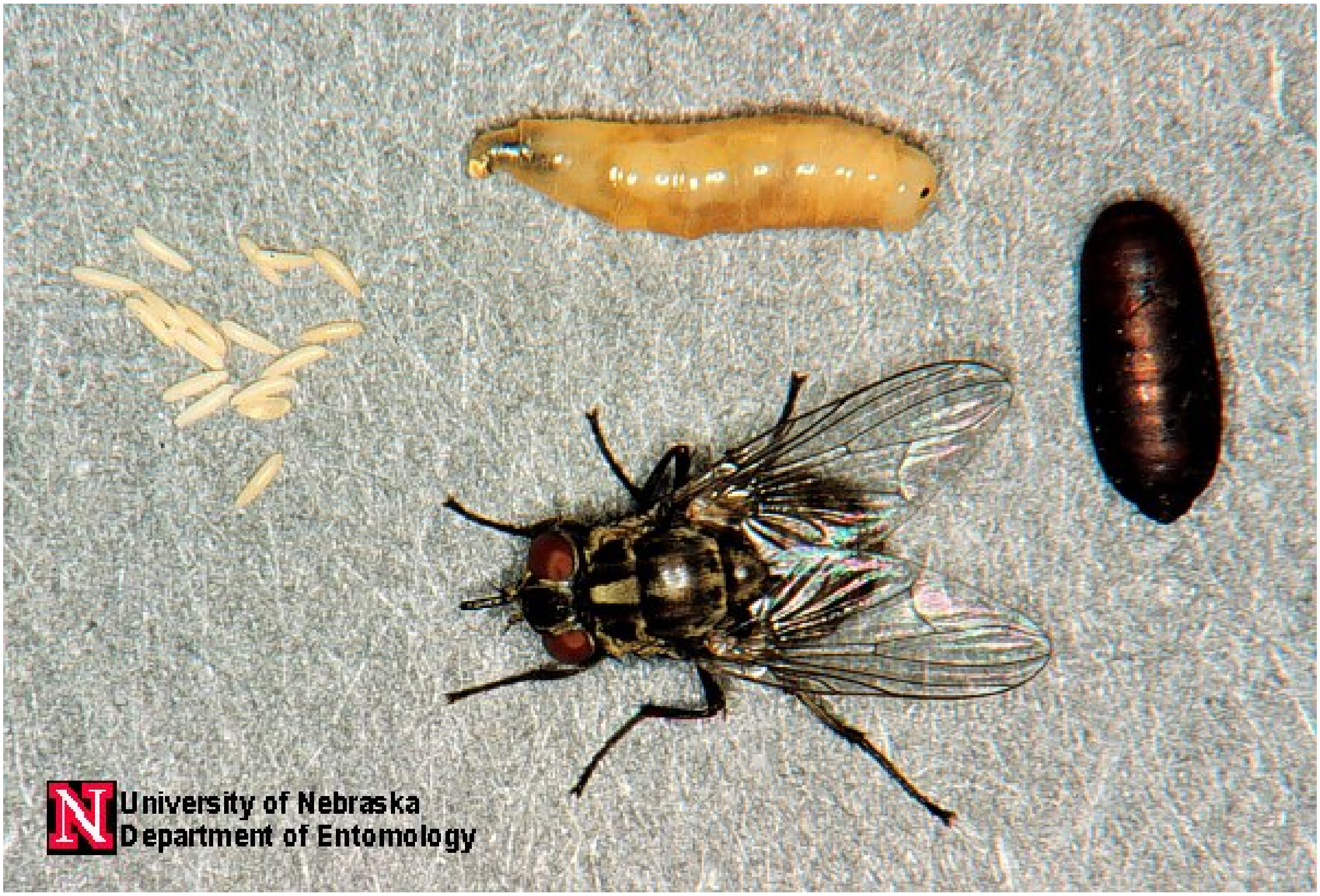


Figure 1. Life Stages of the stable fly, *Stomoxys calcitrans; clockwise from left: eggs, larva, puparium, adult.*

Characteristics

The major morphological feature which distinguishes flies from other insects is their reduced hind wings, termed halteres. The halteres are small, club-like structures that function as balancing organs during flight. Thus adult flies have only one pair of functional wings, hence their scientific name-- Diptera (di - two, pteron - wing). A few other groups of insects have also convergently attained a similar two-winged form, such as male coccoids (Hemiptera-Sternorrhyncha). A few flies have lost their wings (and halteres) altogether.

Because of the reliance on the forewings for flight, the mesothorax has become enlarged to contain the enormous flight muscles, and the pro- and metathorax are correspondingly reduced.

The mouthparts of flies are also characteristically suctorial and many have large fleshy pads with drainage canals termed pseudotracheae for efficient liquid uptake. Some flies have mouthparts modified for stabbing and piercing other insects, such as the predatory robber-flies (Asilidae) and dance flies (Empididae). Mosquitoes and some other ectoparasitic groups have mouthparts modified for piercing the skin of a vertebrate host and removing blood and other fluids.

Figure 2. A robber fly, family Asilidae, with prey.

Larval Diptera are typically small, pale and soft-bodied. They lack true legs and move by peristaltic waves of muscular contraction through the body. The larvae of most species of flies have a reduced head capsule and all that remains are the mandibles and some associated sclerites which are collectively called the cephalopharyngeal skeleton.

Dipteran pupae have non-functional mandibles (adecticous), and may have the appendages free from the body (exarate), or glued to the body (obtect). If exarate, the pupa is concealed inside the hardened skin (puparium) of the last larval instar.

Major Groupings of Diptera

The Diptera are divided into two suborders, the Nematocera and Brachycera. The Nematocera include generally small, delicate insects with long antennae such as mosquitoes, crane-flies, midges and their relatives. The Brachycera includes more compact, robust flies with short antennae. In older classifications two Divisions were recognised in the Brachycera, the Orthorrhapha and Cyclorrhapha. The "Orthorrhapa" includes brachyceran flies with a simple, obtect pupa, such as horse flies and robber flies, and the Cyclorrhapha comprise brachyceran flies with a pupa enclosed in a hardened puparium. The Cyclorrhapha are further divided into two groups based on the presence or absence of the ptilinum and associated fissure on the head. The ptilinum is a sac which is everted during the emergence of the adult fly to assist in breaking free of the puparium. The Aschiza lack the ptilinum whereas it is present in the Schizophora.

Figure 3. *Olbiogaster sackeni*, family Anisopodidae, Nematocera.© 1996 C. R. Nelson

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Figure 4. *Milesia scutellata*, a flower fly, family Syrphidae, Aschiza, Cyclorrhapha.© 1996 C. R. Nelson

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Figure 5. *Paracantha sp.*, a fruit fly, family Tephritidae, Schizophora, Cyclorrhapha.© 1996 C. R. Nelson

Discussion of Phylogenetic Relationships

The traditional groupings of Diptera have been critically reexamined within a cladistic framework in recent decades by a suite of workers, beginning with the great dipterist Willi Hennig. A consensus has emerged that many of the traditional categories such as the Nematocera, Orthorrhapha and Aschiza are not natural groups (they are paraphyletic). In other words these categories consist of a collection of basal lineages from which the other (monophyletic) catergories (Brachycera, Cyclorrhapha and Schizophora, resepectively) arose. Attempts to formulate a monophyletic classification of Diptera have gained pace recently but no overarching consensus has been reached to date (e.g. Michelsen 1996; Oosterbroek and Courtney 1995; Sinclair et al. 1994; Cumming et al. 1995; Griffiths 1994, 1996). The most comprehensive treatment of dipteran phylogeny and contemporary views on morphological character evidence can be found in Volume 3 of the Manual of Nearctic Diptera (McAlpine and Wood 1989).

The addition of data from broad-based comparative morphological studies of both adult and immature stages (for example, Courtney 1991; Sinclair 1992; Ovchinnikova 1989; Oosterbroek and Courtney 1995) and also from DNA sequences will be critical in the reformulation of dipteran classification (Friedrich and Tautz 1997; Wiegmann et al. 2003). The pages at this web site will document the areas of agreement, outstanding difficulties, and research being conducted to derive a new classification. These are exciting times for students of dipteran classification.

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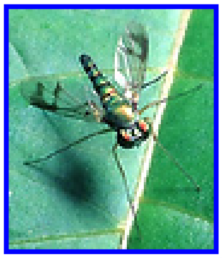
Information on the Internet

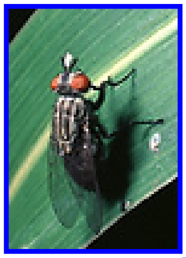
- The Diptera Site, Information about the World's Diptera
- Diptera homepage, Canadian National Collection of Insects, Arachnids, and Nematodes
- World Diptera Systematists HomePage
- Gordon Ramel's Diptera Web Site
- Catalog of the DIPTERA of the Australasian and Oceanian Regions. N.L. Evenhuis
- Catalog of the Fossil Flies of the World. N.L. Evenhuis
- Zweiflügler print from MBL
- UIUC Diptera Images
- Drosophila Flybase
- Flybrain
- FlyView Home (Drosophila Image Database)
- Holdings of Diptera Species at the USNM
- Dipteran Families

Title Illustrations

Scientific Name	Tipula (Lunatipula)
Comments	A crane fly (Tipulidae)
Copyright	© 1996 C. Riley Nelson



Scientific Name	Condylostylus
Comments	A long-legged fly (Dolichopodidae)
Copyright	© 1996 C. Riley Nelson



Scientific Name	Calodexia
Location	Costa Rica
Comments	A parasitoid fly (Tachinidae), host: army ants
Copyright	© 1996 C. Riley Nelson

About This Page

The authors wish to thank C.R. Nelsen, N.L. Evenhuis and D. Maddison for comments and suggestions on this page. We also thank C.R. Nelson, M. Stringham, S.J. Scheffer, D. Sear, and J. Baker for providing photographic images.

Brian M. Wiegmann
bwiegman@unity.ncsu.edu
Department of Entomology, Box 7613, North Carolina State University, Raleigh, NC 27695

David K. Yeates
david.yeates@ento.csiro.au
CSIRO Division of Entomology, PO Box 1700, Canberra ACT 2601

Correspondence regarding this page should be directed to Brian M. Wiegmann at bwiegman@unity.ncsu.edu

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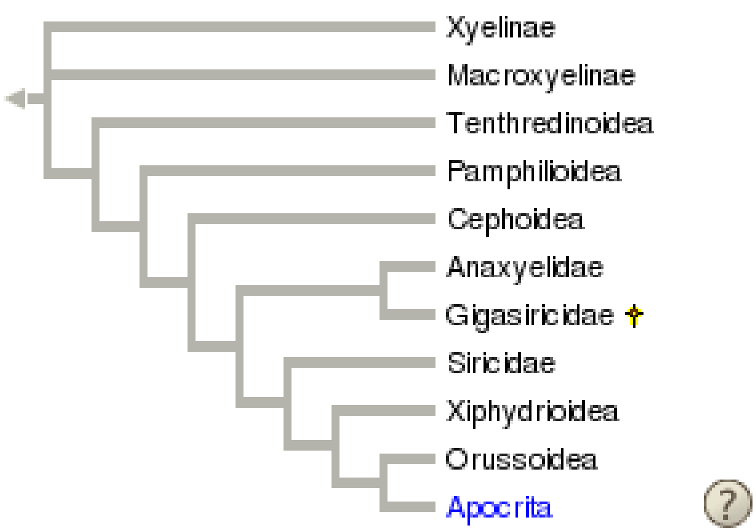
Hymenoptera

Wasps, ants, bees, and sawflies



Tree after Ronquist et al. (1999), Schulmeister (2003), Sharkey and Roy (2002), and Vilhelmsen (1997, 2001).

Containing group: Endopterygota

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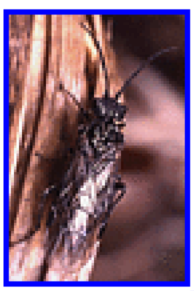
- The International Society of Hymenopterists
- Hymenoptera Name Server (Ohio State University)
- The Social Insects Web (American Museum of Natural History)
- Cal Academy Hymenoptera
- CSIRO Hymenoptera Ecowatch
- Hymenoptera Families (INBIO, Costa Rica)
- Introduction to the Hymenoptera at UCMP Berkeley
- Introduction to the Hymenoptera (USDA)

Title Illustrations

Scientific Name	Rhyssa persuasoria
Acknowledgements	Photograph courtesy InsectImages.org (#9008009)
Specimen Condition	Live Specimen
Behavior	giant ichneumon wasp boring the surface of fir trunk infested with wood wasp larvae
Sex	Female
Life Cycle Stage	adult
Copyright	© Boris Hrasovec, University of Zagreb

Scientific Name	Halictidae
Location	Michigan, USA
Specimen Condition	Live Specimen
Copyright	© 1995 Joseph L. Spencer



Scientific Name	Tenthredinidae
Location	Michigan, USA
Comments	A sawfly
Specimen Condition	Live Specimen
Copyright	© 1995 Joseph L. Spencer

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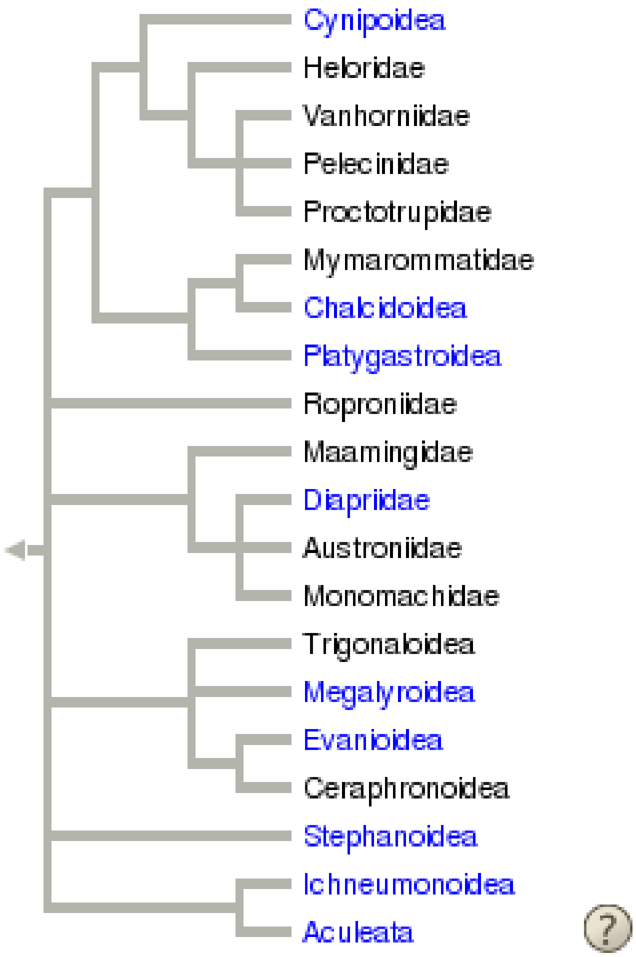
Wasps



Tree after Dowton and Austin (2001), Ronquist (1999), Sharkey and Roy (2002), and Whitfield (1998).

Containing group: Hymenoptera

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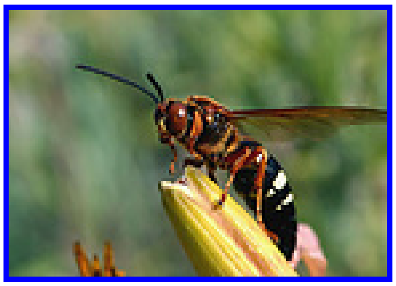
Information on the Internet

- Research on Biocontrol at the Institute of Zoology, Kiev, Ukraine

Title Illustrations

Scientific Name	Pelecinus sp. (Pelecinidae)
Location	Ecuador
Specimen Condition	Live Specimen
Sex	Female
Copyright	© 2003 Alex Wild



Scientific Name	Sphecius speciosus (Aculeata: Sphecidae)
Location	Kansas, USA
Comments	Cicada killer
Specimen Condition	Live Specimen
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Insect Fossils Classification with Hexapoda

Fossil Insect Classification

Class Insecta and Subphylum Hexapoda

Unlike the trilobite that has left a prodigious fossil record, the preservation of insects in sedimentary matrix is relatively rare, and essentially limited to the Laggerstat sites. The reason for the scarcity of insect fossil is the poor preservation potential of the insect's exoskeleton. Like other Arthropods, insects have an external skeleton called an exoskeleton. Unlike the thick and calcified trilobite exoskeleton, the insect exoskeleton is made of a thin, plastic-like material called chitin, along with a tough protein. This thin, waterproof covering simple does not preserve well in most oxygenated environments, making insect fossils sparse despite the tremendous number that could have been preserved. The exception is in fossil resinite (amber, by street name), where it is possible for even the minutest details to be preserved. Despite their huge strength to weight ratio, insects were often to small to escape the sticky resin exuded by trees, and which later became a fossil itself, with physical properties akin to modern polymerized plastics.

Insect evolution is a powerful illustration of decent with modification. The earliest known insects are tiny wingless forms from the early and middle Devonian. Insect flight developed with suddenness resembling the Cambrian explosion during the middle Carboniferous, apparently the result of the significant survival advantage that was accrued. By the end of the Carboniferous, the subphylum insecta had evolved into a large number of distinct orders. During the Permian, new insects forms appeared. Blattoid and Orthopteroid orders attained their greatest diversity, and new groups like the Psocoptera, homopteran Hemiptera, Mecoptera and Coleoptera became ubiquitous and diverse. The Permian extinction wiped out nine orders of insects, and more orders disappeared in the Triassic or the early Jurassic. However, surviving orders such as Neuroptera, Mecoptera, and Diptera, and Coleoptera underwent further adaptive radiation establishing many families extant in modern times. So exquisite is insect design that most groups were well formed by the Cretaceous and remain largely unchanged in appearance during modern times.

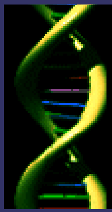
Insect evolution has led to prodigious diversity of this animal group comapred with other members of Domain Eucarya. For example, there are believed to be three times as many Dipetran species (fllies) as there are vertebrate species, and ten times as many Coliopteran species (beetles) as vertebrate species.

Taxonomic research on fossil insects has always been relegated to a subordinate role when compared to that of living species. There are large numbers of undetermined fossil insects in many collections throughout the world awaiting descriptions, but only a small fraction of systematic research has ever been devoted to these fossils.

Class Insecta Classification with Hexapoda

Great clade	Class	Subclass	Division	Order	Common Names within order	Appearance of Order	Approximate Extant species described
Apterygotes (without wings)	Collembola				Springtail	Devonian	2,000
	Proturan				Proturan	Devonian	rare/100
	Dipluran				Dipluan	Carboniferous	rare/100
	Archaeognatha				Bristletail	Upper Silurian	700 named species
	Thysanura				Silverfish	Lower Devonian	
		Palaeopterans		Ephemeroptera	Mayfly	Devonian	2,100

Pterygota (Have or had wings)			Odonata	Dragonfly; Damselfly	Devonian	>5,500
	Neoptera	Orthopterodea	Blattodea	Cockroach	Mississippian	3,700
			Mantodea	Mantid	Pennsylvannian	>1,800
			Mantophasmatodea	Gladiator	-	-
			Isoptera	Termite	Upper Cretaceous	2,000
			Plecoptera	Stonefly	Permian	1,600
			Orthoptera	Grasshopper; locust; cricket	Mississippian	20,000
			Dermaptera	Earwig	Jurrasic	2,000
			Embioptera	webspinners		170
			Phasmida	Walking stick; walking leaf	Lower Triassic	2,500
		Hemipterodea	Psocoptera	Book and bark lice	Permian	6,000
			Hemiptera	True bugs	Upper Pennsylvannian	82,000
			Homoptera	Cicada; aphid; plant hopper; leaf hopper; spittlebugs; scale insects; mealy bugs	Permian	33,000
		Holometabola	Coleoptera	Beetles	Middle Permian	350,000
			Neuroptera	Lacewing; antlion; snakefly	Lower Permian	4,700
			Hymenoptera	Ant; bee; wasp; sawfly	Upper Triassic	130,000
			Mecoptera	Scorpian fly	Pennsylvannian	500
			Siphonoptera	Flea	Miocene	1,750
			Diptera	Fly; mosquito; gnat	Middle Triassic	150,000
			Trichoptera	Caddisfly	Lower Triassic	7,000
			Lepidoptera	Butterfly; moth	Upper Cretaceous	120,000



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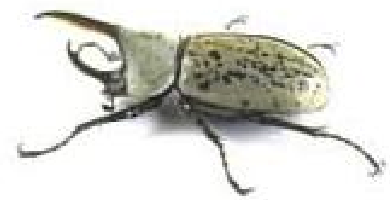
Coleoptera

The Beetles



QUICK REFERENCE
> Butterflies & Moths
> Beetles
> Bees, Wasps, & Ants
> Crickets & Grasshoppers
> Flies
> Walking-sticks/leaves
> Aerial Insects
> Very Small Insects
> Other Insects
> Spiders & Non-Insects

[HOW TO ORDER]

The beetles are the most successful group of complex animals on Earth, forming almost one third of all described animal species and about two fifths of all insects. When the British scientist J.B.S. Haldane was asked what could be learned about "God" from the study of "His" creations, he purportedly replied, "..an inordinate fondness for beetles." - with 300,000 known species, that seems fairly accurate. Designed to fit all sorts of ecological niches, beetle diversity is extreme. They costume themselves with countless combinations and variations of color and texture; spikes and horns. They range in size from 0.25mm to 20cm (0.01" to 8") and occur in almost all habitats throughout the world, feasting on a wide variety of resources too diverse to list. This versatility allows them to be found in such places as the black depths of caves, beneath the surface of fresh water, within human dwellings and in the bowels of ant colonies, where they live as commensal guests. Some have even become parasites, exploiting other insect species. According to the fossil record, beetles first appeared during the Permian period, about 280 million years ago. The word "Coleoptera" is derived from the ancient Greek words for, "sheath-wing", referring to the characteristic thickened forewings, called "elytra". In most families elytra are hard and protect the hindwings, which remain folded beneath when the beetle is at rest. The delicate hindwings are brought out only when the beetle wishes to fly. Although most beetles have wings and the power of flight, some species have devolved and lost these attributes. All beetles pass through a larval stage. As larvae, they lead a multitude of different lives, depending on the species. Some larvae have well-formed legs and those of many predatory species are highly active, hunting other arthropods from the moment they are born. Those that live hidden, burrowing existences are known as grubs. Other kinds of beetle larvae are: wireworms, mealworms, woolly bears (this name is also shared by a caterpillar) and glow-worms. As a final note, we wish to say that all the colors of the beetles on view here are real, even the gold and silver hues. Although these colors may seem unearthly, the fabulous metallic sheens and shimmering iridescence are caused by simple optical interference, such as it occurs in a diffraction grating.

[View All Coleoptera Specimens]


Adephaga


Carabidae
Ground Beetles


Cicindelidae
Tiger Beetles


Dytiscidae
Predaceous Diving Beetles


Gyrinidae
Whirligig Beetles

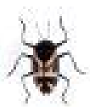
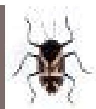

Polyphaga


Buprestoidea


Buprestidae
The Jewel Beetles

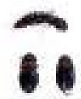

Cantharoidea

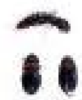

Lampyridae
Fireflies or Lightning Bugs

-  *Chrysomeloidea*
  -  *Cerambycidae* Long-horned Beetles
    -  *Cerambycinae*
    -  *Lamiinae*
    -  *Prioninae*
  -  *Chrysomelidae* Leaf Beetles
-  *Cleroidea*
  -  *Trogostidae* Bark-gnawing beetles
-  *Cucujoidea*
  -  *Erotylidae* Pleasing Fungus Beetles
-  *Curculionoidea*


Brentidae
Primitive Weevils


Curculionidae
True Weevils or Snout Beetles


Dermestoidea

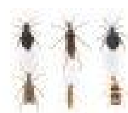

Dermestidae
Larder and Museum Beetles

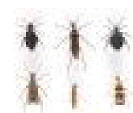

Elateroidea

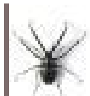

Elateridae
Click Beetles

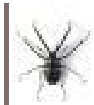

Hydrophiloidea


Hydrophilidae
Water Scavenger Beetles


Melooidea


Meloidae
Blister Beetles

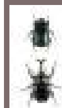

Scarabaeoidea

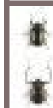

Lucanidae
Stag Beetles


Passalidae
Passalid or Peg Beetles


Scarabaeidae
Scarab Beetles

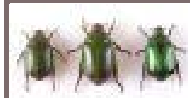

Cetoniinae
Flower Beetles


Dynastinae
Rhinoceros Beetles


Euchirinae
Long-armed Chafers


Geotrupinae
Earth-boring Dung Beetles


Melolonthinae
June Beetles and Chafers

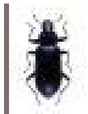

Rutelinae
Shining Leaf Chafers


Scarabaeinae
Dung Beetles and Tumblebugs


Staphylinoidea

Silphidae
Carrion Beetles

Staphylinidae
Rove Beetles



Tenebrionoidea

Tenebrionidae
Darkling Beetles

Trictenotomidae
Log-boring Beetles

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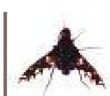
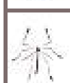
[HOW TO ORDER]

Diptera

The Flies

Around since the Permian period (225-280 million years ago), flies are one of the most ubiquitous insects. They are found on every continent, including Antarctica (a rare boast indeed!). In fact, the wingless midge Belgica antarctica is Antarctica's only indigenous insect and at 1.3cm (0.5"), Antarctica's second largest terrestrial animal (beaten only by a slightly larger springtail)! It should also be noted that flies are the stowaways that turn up most often at McMurdo Station. Adaptable and resilient, flies are one of the few insects that can thrive under cool conditions, often making up a quarter of the insect population in temperate regions. In addition, many kinds of flies are associated with marine habitats, generally feeding along the littoral zone on algae or rotting seaweed. However, flightless midges in the genus Pontomyia (found throughout the Indo-Pacific) have dared to go where no insects tread: the depths of the ocean! Adult males skate around on the surface of the sea where they seek out the strange larvae-like females. Eggs are laid immediately after mating (embedded in a gelatinous matrix) as a long coil, which sinks to the bottom. Larvae feed at depths of up to 30 meters! Pupae float back to the surface shortly before emergence. To top it all off, these midges have the shortest adult life span of all known insects: a mere 30 minutes to 3 hours! Flies stand out among other insects by having only a single pair of wings. The word Diptera comes from the Greek words for "two-wing", making reference to this unique phenomenon (all other winged insects, except the mysterious Stylopids, have two pairs of wings). The fly's other pair of wings has evolved into structures called "halteres". Sense organs in the bases of these halteres allow them to act as gyroscopes, telling the fly how fast it is flying or turning and whether or not it is being blown off course. Flies do not have chewing mouthparts. Instead, with the aid of powerful pumps in their heads, a fly's mouthparts are adapted for sucking up liquefied nutrients. Although often repulsive in their choice of food, they play an important role in the environment and help to keep Earth from becoming a huge sphere of rotting biomass. With about 90,000 known species, fly larvae (maggots) consume all kinds of unpleasant things; fungi, dung, animal corpses and all manner of foul, rotten, organic material. Other kinds of maggots are parasitic; some feeding within the bodies of mammalian hosts while others mine the roots, stems, and leaves of plants. Adult flies live as many interesting, varied lives as their larvae, generally relying on food sources very different from that of the larvae. A classic example of this is the mosquito. As an adult, the males feed on nectar and the females on blood. The larvae however, live in shallow, fresh water, feeding on organic detritus, algae and tiny, aquatic organisms. Many species of flies that are known vectors for disease are still considered a pest throughout much of Earth's equatorial lands. Looking on the bright side, it is a kind of tiny fly, a midge (Forcipomyia[=Rhynchoforcipomyia]spp.), that is the sole pollinator of the cacao tree, the only known source of cacao (the main component of chocolate)!

[View All Diptera Specimens]

	*Brachycera* The Short-Horned Flies
	*Cyclorrhapha* The Higher Flies
	*Nematocera* The Thread-Horned Flies

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[HOW TO ORDER]

Hymenoptera

The Ants, Bees, Wasps and Sawflies

The order Hymenoptera includes the familiar bees and wasps as well as the ants and sawflies. Ants evolved from prehistoric wasps, yet many people are unaware of the close kinship that ants share with their winged cousins. It is not known when the the two groups diverged but recent genetic evidence indicates it was at least 100 million years ago. The word "Hymenoptera" comes from the Greek words for "membrane-wing", referring to the transparent, sparsely veined wings. Hymenopterans have two pairs of these wings (wings are present in ants but only in the reproductive castes) and mouthparts designed for cutting and chewing. All Hymenopterans begin life as grub-like larvae (in social species, they are helpless and must be cared for and fed by the adults), later pupating into their adult forms. Social behavior evolved 11 times within the Hymenoptera while it occurred only once in all the other insects (termites). Among these social species, there is a tendency towards female-dominated societies, with males used only for procreation. Hymenopterans have developed not only some of the most complicated animal societies but also many of the most intricate life-cycles known in the insect kingdom. Tens of thousands of species of wasps live solitary existences of complex parasitism. Some of these parasites can parasitize other parasites within the bodies of the doomed host! Talk about evolution. The Hymenopterans are considered major benefactors of humankind: pollinating hundreds of crops, controlling numerous insect pest species through parasitism, and creating the unique delicacy that humans call honey. The oldest fossil Hymenopteran, a sawfly, dates back to the Triassic period, 225-195 million years ago. It is believed that the Hymenoptera evolved from the scorpionflies (Mecoptera), somewhere back in the mists of time. There are at least 280,000 known species of Hymenopterans.

[View All Hymenoptera Specimens]

Apocrita
The Parasitic Wasps, Wasps, Ants and Bees

Ichneumonoidea
Braconid & Ichneumon Wasps

Ichneumonidae
Ichneumon Wasps AKA Ichneumon Flies

Proctotrupoidea

Pelecinidae
The Pelecinids

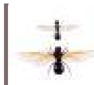

Sphecoidea
Bees & Solitary Wasps

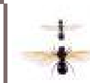

Ampulicidae
Thread-waisted Wasps


Anthophoridae
Carpenter Bees


Apidae
Honeybees, Bumblebees & Orchid Bees


Sphecidae
Sphecid Wasps

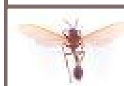

Vespoidea
Ants, Social Wasps and Giant Hunting Wasps

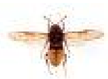

Formicidae
True Ants


Mutillidae
Velvet Ants


Pompilidae
Spider-hunting Wasps


Scoliidae
Scoliid Wasps


Vespidae
Hornets, Yellow Jackets & Paper Wasps


Symphyta
The Sawflies, Horntails, and Woodwasps

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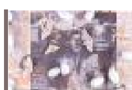
Lepidoptera

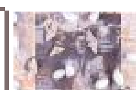
The Butterflies and Moths

The order Lepidoptera is comprised of the butterflies and moths, with the number of known species climbing towards 200,000. Fossil records are scarce and only go back to the late Cretaceous, some 100 to 130 million years ago. It is widely accepted that Lepidopterans evolved long before that, from an insect ancestor similar to caddisflies (Trichoptera). Although primitive moths in the suborder Zeugloptera still retain chewing mouth parts, most moths and butterflies have long since developed a proboscis with which to feed. The order's name, Lepidoptera, is derived from Greek words meaning, "scale-wing". This refers to the arrangement of tiny overlapping scales (like shingles on a roof) that color the surface of most Lepidopterans wings. These scales contain the pigments (available in every color of the rainbow) which create so many startling patterns of color and inexplicable beauty. When modified to reflect only one wavelength of light, they become responsible for the iridescence seen on some species, like the Morpho butterflies. It is a sad reality that most people believe that butterflies are beautiful and moths are ugly. Take a look at a Sunset Moth and you'll realize that belief couldn't be more false. Moths and butterflies are viewed to be as different as night and day, when in fact they are very closely related. Castniid moths look so much like butterflies that they were once thought to be direct ancestors of the skippers (the most primitive of the butterflies and directly related to the moths). All moths and butterflies begin their lives as caterpillars. In order to complete metamorphosis, they must pupate. Moths will often spin cocoons (something which butterflies cannot do) but many simply pass through this stage as bare pupae buried in soil. In contrast, it is butterflies who alone create the fabulous structures known as chrysalids. While butterflies may have the upper hand as far as color diversity they only make up about 10% of the Lepidoptera. Moths are diverse and far more spectacular as a whole. There are many beautiful moths and anyone looking for colorful Lepidoptera should not overlook them.

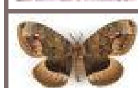
[View All Lepidoptera Specimens]



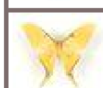
Bombycoidea
The Emperors and Silk Moths



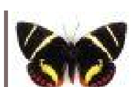
Bombycidae
Silk Moths



Brahmaeidae
Brahmaeid Moths



Saturniidae
Giant Silkmoths



Castnioidea

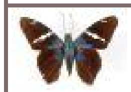

Castniidae
Castniid Moths


Geometroidea
The Geometers, Loopers and Relatives


Geometridae
Measuring-worm Moths

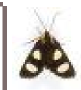

Uraniidae
Uraniid Moths

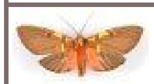

Hepialoidea
The Ghost and Swift Moths


Hesperoidea
The Skippers


Hesperiidae
The True Skippers

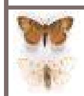

Noctuoidea


Agaristidae
Agaristid Moths


Arctiidae
Arctiid Moths


Ctenuchidae
Ctenuchid Moths


Hypsidae (=Pericopidae)
Hypsid Moths


Lymantriidae
Lymantriid Moths


Noctuidae
Noctid Moths


Notodontoidea

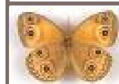

Notodontidae
Prominent Moths

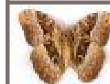

Papilionoidea
The Butterflies

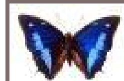

Lycaenidae
The Blues, Coppers and Hairstreaks


Nymphalidae
The Brushfooted Butterflies

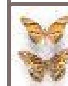

Acraeinae
The Acrea Butterflies


Amathusiinae
Saturns, Palm-kings and Jungle Glories

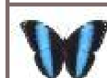

Brassolinae
The Owl Butterflies

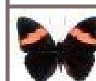

Charaxiinae
The Charaxin Butterflies

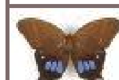

Danainae
The Milkweed Butterflies


Heliconiinae
The Passionvine or Longwing Butterflies


Ithomiinae
The Ithomin Butterflies


Morphiinae
The Morpho Butterflies


Nymphalinae
The Nymphalin Butterflies


Satyrinae
Satyrs and Woodnymphs


Papilionidae
The Birdwings, Swallowtails, Apollos and Festoons


[Pieridae](#)
The Whites, Jezebels, Sulphurs and Yellows


[Riodinidae](#)
The Metalmarks, Judies and Snout Butterflies


[Sphingoidea](#)
The Sphinx or Hawk Moths


[Sphingidae](#)
The Sphinx Moths


[Tineoidea](#)
The Clothes Moths, Bagworms and Relatives


[Psychidae](#)
Psychid Moths AKA Bagworms


[Yponomeutoidea](#)
The Web Spinners and Relatives


[Sesiidae](#)


[Zygaenoidea](#)
The Burnets, Foresters and Relatives


[Zygaenidae](#)
Zygaenid Moths

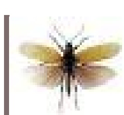
  Contact us: contact@godofinsects.com

Orthoptera

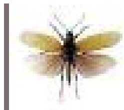
The Grasshoppers, Crickets and Katydids

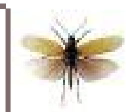
The order Orthoptera contains the familiar grasshoppers, locusts, crickets, and katydids. The name "Orthoptera" is derived from the Greek words for “straight-wing”. The ancestors of the Orthoptera share a common lineage with cockroaches; their origins go back to the Carboniferous period some 345-280 million years ago. The earliest fossils found so far date from about 300 million years ago. Orthopterans exhibit incomplete metamorphosis, meaning that the newly hatched nymphs resemble tiny versions of the adults. Amongst the crickets, nymphs will very often be tiny, wingless versions of the adults but amongst the grasshoppers, nymphs are often brightly colored with bold patterns that do not resemble the adults colors. This is to advertise their toxicity (the result of feeding on poisonous plants) to predators. Orthopterans are an interesting group with well over 20,000 described species. Many are well-known for their sound-producing capabilities and the order also contains some of the largest insects. A few of the massive Orthopterans that inhabit the world, many unchanged since the days of the Dinosaurs, are: giant wetas weighing 70 grams, giant katydids as big as a human hand, giant grasshoppers with 12” wingspans (30cm). Given the amazing variety of forms scientists have broken them down into two Suborders: Caelifera and Ensifera.

[View All Orthoptera Specimens]



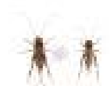
Caelifera
The Grasshoppers

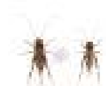

Acridoidea

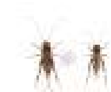

Acrididae
Short-horned AKA Common Grasshoppers


Proscopiidae
Stick Grasshoppers


Tetrigidae
Ground-hoppers, Pygmy Grasshoppers and Grouse Locusts

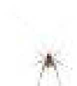

Ensifera
The Crickets


Grylloidea


Gryllidae
True Crickets


Gryllotalpidae
Mole-crickets


Tettigonioidea


Raphidophoridae
Camel and cave Crickets


Tettigoniidae
Katydids and Bush Crickets