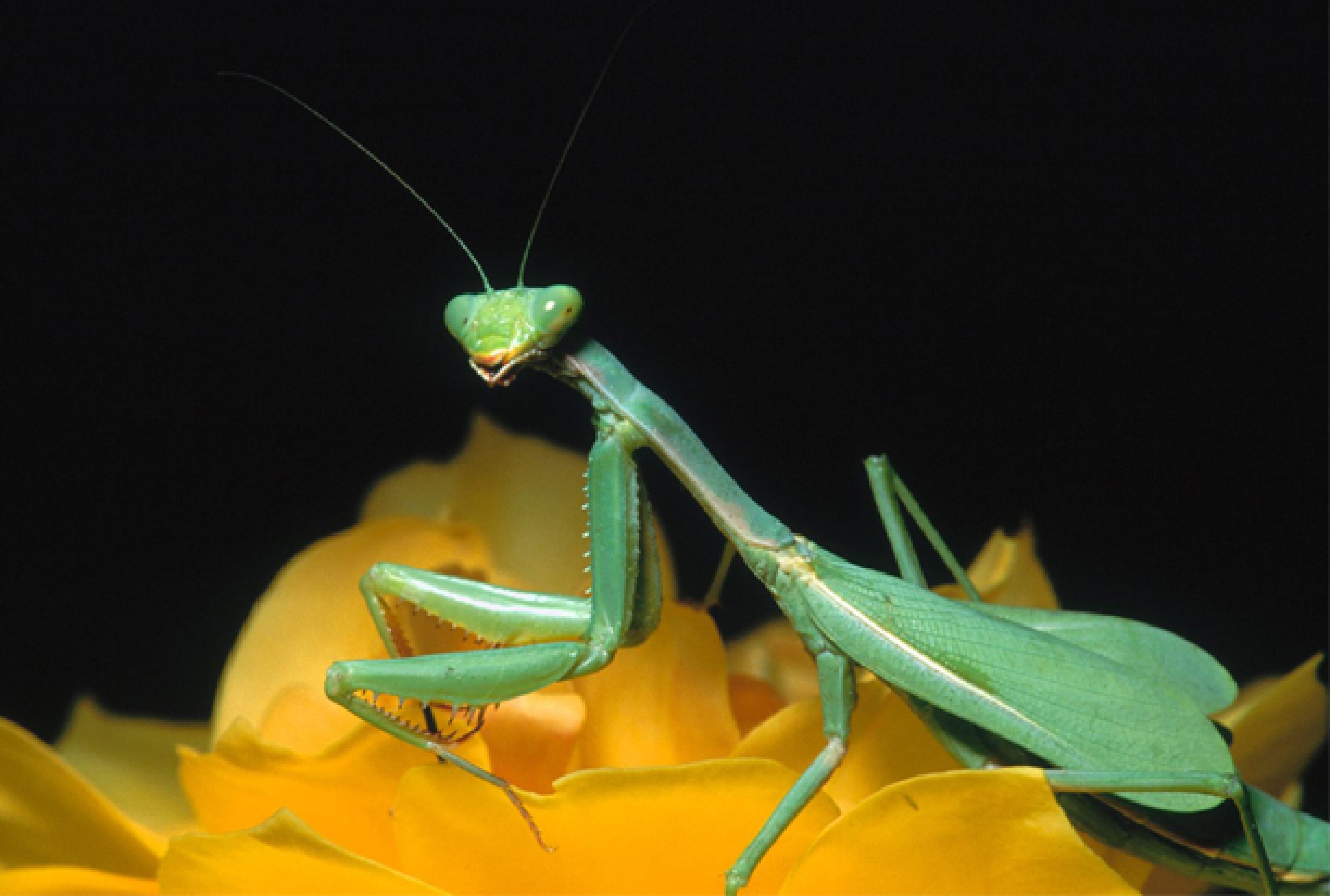
Classification of Insects

Sandra Dellinger



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Chapter 1

Mantis

Mantodea Temporal range: 145–0 Ma Cretaceous–Recent	

Sphodromantis viridis

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Subclass:	Pterygota
Infraclass:	Neoptera
Superorder:	Dictyoptera
Order:	**Mantodea** Burmeister, 1838

Families

Chaeteessidae
Metallyticidae
Mantoididae
Amorphoscelididae

Eremiaphilidae
Hymenopodidae
Liturgusidae
Mantidae
Empusidae

Synonyms

- Manteodea Burmeister, 1829
- Mantearia
- Mantoptera

Mantodea or **mantises** is an order of insects that contains approximately 2,200 species in nine families worldwide in temperate and tropical habitats. Most of the species are in the family Mantidae. Historically, the term "mantid" was used to refer to any member of the order because for most of the past century, only one family was recognized within the order; technically, however, the term only refers to this one family, meaning the species in the other eight recently established families are not mantids, by definition (i.e., they are empusids, or hymenopodids, etc.), and the term "mantises" should be used when referring to the entire order.

A colloquial name for the order is "**praying mantises**", because of the typical "prayer-like" stance, although the term is often misspelled as "preying mantis" since mantises are predatory. In Europe, the name "praying mantis" refers to *Mantis religiosa*. The closest relatives of mantises are the orders Isoptera (termites) and Blattodea (cockroaches), and these three groups together are sometimes ranked as an order rather than a superorder. They are sometimes confused with phasmids (stick/leaf insects) and other elongated insects such as grasshoppers and crickets.

Etymology

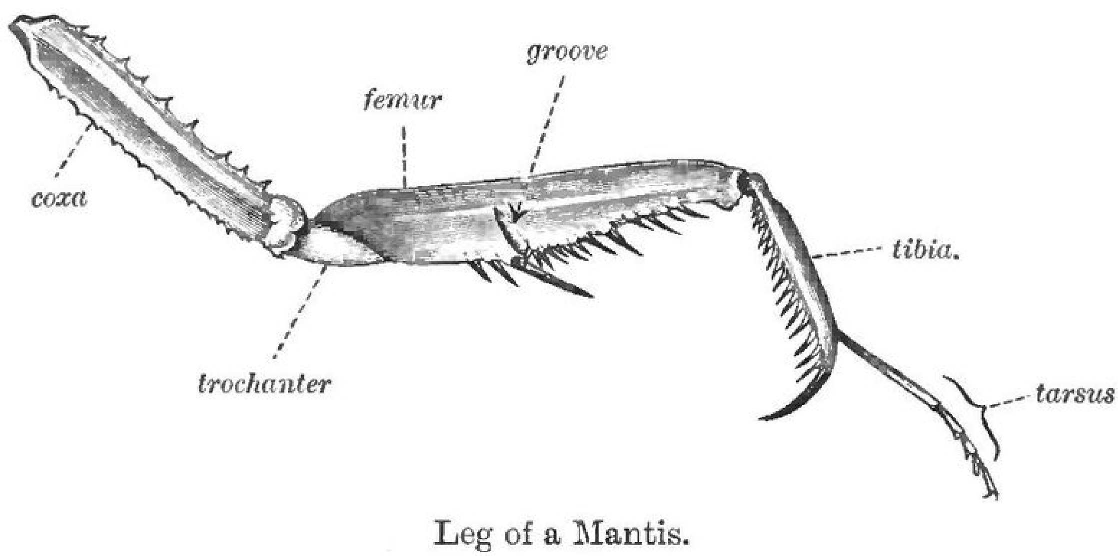
The scientific name Mantodea comes from the Greek words μάντις meaning a prophet, and εἶδος for form or shape. The name was coined in 1838 by the German entomologist Hermann Burmeister. The common term mantis is also from the Greek word μάντις for prophet.

Systematics

The systematics of mantises have long been disputed. Mantises, along with walking sticks, were once placed in the order Orthoptera with the cockroaches (now Blattodea) and rock crawlers (now Grylloblattodea). Kristensen (1991) combined Mantodea with the cockroaches and termites into the order Dictyoptera.

Anatomy and morphology

Close up image of a mantis' face (*Archimantis latistyla*) showing its compound eyes and labrum. The structure of the compound eye creates the illusion of a small pupil.



The foreleg modifications

Mantises have two grasping, spiked forelegs ("raptorial legs") in which prey items are caught and held securely. The first thoracic segment, the prothorax, is commonly elongated and flexibly articulated, allowing for greater range of movement of the front limbs, while the remainder of the body remains more or less immobile. The articulation of the head is also remarkably flexible, permitting nearly 300 degrees of movement in some species, allowing for a great range of vision (their compound eyes have a large binocular field of vision) without having to move the remainder of the body. As their hunting relies heavily on vision, they are primarily diurnal, but many species will fly at night.

Evolution

Some believe that mantises evolved from proto-cockroaches, diverging from their common ancestors by the Cretaceous period, possibly from species like *Raphidiomimula burmitica*, a predatory cockroach with mantis-like forelegs. Possibly the earliest known modern mantis is *Regiata scutra*, although more common (and confirmed) is *Santanmantis*, a stilt-legged genus, also from the Cretaceous. Like their close termite cousins, though, mantises did not become common and diverse until the early Tertiary period.

Behaviour

Diet and predatory behaviour

Tenodera sinensis preying on a cricket

Mantises are exclusively predatory. Insects form the primary diet, but larger species have been known to prey on small lizards, frogs, birds, snakes, fish, and even rodents; they will prey upon any species small enough to successfully capture and devour. Most species of mantis are known to engage in cannibalism. The majority of mantises are ambush predators, waiting for prey to stray too near. The mantis then lashes out at remarkable speed. Some ground and bark species, however, pursue their prey rather quickly. Prey items are caught and held securely with grasping, spiked forelegs.

Defense and camouflage

Species in genus *Choeradodis* have laterally expanded thoraxes for leaf mimicry.

Generally, mantises are protected simply by virtue of concealment. When directly threatened, many mantis species stand tall and spread their forelegs, with their wings fanning out wide. The fanning of the wings evidently makes the mantis seem larger and more threatening, with some species having bright colors and patterns on their hind wings and inner surfaces of their front legs for this purpose. If harassment persists, a mantis may then strike with its forelegs and attempt to pinch or bite. As part of the threat display, some species also may produce a hissing sound by expelling air from the abdominal spiracles. When flying at night, at least some mantises are able to detect the echolocation sounds produced by bats, and when the frequency begins to increase rapidly, indicating an approaching bat, they will stop flying horizontally and begin a descending spiral toward the safety of the ground, often preceded by an aerial loop or spin.

Mantises, like stick insects, show rocking behaviour in which the insect makes rhythmic, repetitive side-to-side movements. Functions proposed for this behaviour include the enhancement of crypsis by means of the resemblance to vegetation moving in the wind. However, the repetitive swaying movements may be most important in allowing the insects to discriminate objects from the background by their relative movement, a visual mechanism typical of simpler animals. Rocking movements by these generally sedentary insects may replace flying or running as a source of relative motion of objects in the visual field.

Mantises are camouflaged, and most species make use of protective coloration to blend in with the foliage or substrate, both to avoid predators themselves, and to better snare their victims. Various species have evolved to not only blend with the foliage, but to mimic it, appearing as either living or withered leaves, sticks, tree bark, blades of grass, flowers, or even stones. Some species in Africa and Australia are able to turn black after a molt following a fire in the region to blend in with the fire ravaged landscape (fire melanism). While mantises can bite, they have no venom. They can also slash captors with their raptorial legs (which is often preceded by a threat display wherein the mantis will rear back and spread its front legs and wings (if present), often revealing vivid colors and/or eyespots to startle a predator). They do not appear to be chemically protected; nearly any large predatory animal will eat a mantis such as Scops owls, shrikes, bullfrogs, chameleons, and milk snakes.

Reproduction and life history

Mantis religiosa mating (top male, bottom female)

A recently laid mantis ootheca

In some species of mantis, nymphs survive with the help of ant mimicry

Sexual cannibalism is common among mantises in captivity, and under some circumstances may also be observed in the field. The female may start feeding by biting off the male's head (as they do with regular prey), and if mating had begun, the male's movements may become even more vigorous in its delivery of sperm. Early researchers thought that because copulatory movement is controlled by a ganglion in the abdomen, not the head, removal of the male's head was a reproductive strategy by females to enhance fertilisation while obtaining sustenance. Later, this behaviour appeared to be an artifact of intrusive laboratory observation. Whether the behaviour in the field is natural, or also the result of distractions caused by the human observer, remains controversial. Mantises are highly visual organisms, and notice any disturbance occurring in the laboratory or field such as bright lights or moving scientists. Research by Liske and Davis (1984) and others found (e.g. using video recorders in vacant rooms) that Chinese mantises that had been fed *ad libitum* (so that they were not hungry) actually displayed elaborate courtship behaviour when left undisturbed. The male engages the female in courtship dance, to change her interest from feeding to mating. Courtship display has also been observed in other species, but it does not hold for all mantises.

The reason for sexual cannibalism has been debated, with some considering submissive males to be achieving a selective advantage in their ability to produce offspring. This theory is supported by a quantifiable increase in the duration of copulation among males who are cannibalized, in some cases doubling both the duration and the chance of fertilization. This is further supported in a study where males were seen to approach hungry females with more caution, and were shown to remain mounted on hungry females for a longer time, indicating that males actively avoiding cannibalism may mate with multiple females. The act of dismounting is one of the most dangerous times for males during copulation, for it is at this time that females most frequently cannibalize their mates. This increase in mounting duration was thought to indicate that males would be more prone to wait for an opportune time to dismount from a hungry female rather than from a satiated female that would be less likely to cannibalize her mate. Some consider this to be an indication that male submissiveness does not inherently increase male reproductive success, rather that more fit males are likely to approach a female with caution and escape.

The mating season in temperate climates typically begins in autumn. To mate following courtship, the male usually leaps onto the female's back, and clasps her thorax and wing bases with his forelegs. He then arches his abdomen to deposit and store sperm in a special chamber near the tip of the female's abdomen. The female then lays between 10 and 400 eggs, depending on the species. Eggs are typically deposited in a frothy mass that is produced by glands in the abdomen. This froth then hardens, creating a protective capsule with a further protective coat, and the egg mass is called an ootheca. Depending on the species these can be attached to a flat surface, wrapped around a plant or even deposited in the ground. Despite the versatility and durability of the eggs, they are often preyed on, especially by several species of parasitic wasps. In a few species, the mother guards the eggs.

As in related insect groups, mantises go through three stages of metamorphosis: egg, nymph, and adult (mantises are among the hemimetabolic insects). The nymph and adult insect are structurally quite similar, except that the nymph is smaller and has no wings or functional genitalia. The nymphs are also sometimes colored differently from the adult, and the early stages are often mimics of ants. A mantis nymph increases in size (often changing its diet as it does so) by replacing its outer body covering with a sturdy, flexible exoskeleton and molting when needed. This can happen up to five to ten times, depending on the species. After the final molt most species have wings, though some species are wingless or brachypterous ("short-winged"), particularly in the female sex.

In tropical species, the natural lifespan of a mantis in the wild is about 10–12 months, but some species kept in captivity have been sustained for 14 months. In colder areas, females will die during the winter (as well as any surviving males).

Pest control uses

Organic gardeners who avoid pesticides may encourage mantises as a form of biological pest control. Tens of thousands of mantis egg cases are sold each year in some garden stores for this purpose.

During fall, praying mantis females deposit a sticky egg case on the underside of a leaf or on a twig. If the egg case survives winter, the offspring, called nymphs, emerge in late spring or early summer. The nymphs have voracious appetites and typically cannibalize each other if they don't have an adequate supply of aphids and other small insects. Egg cases are commercially available for placement in landscaping.

However, mantises prey on neutral and beneficial insects as well, basically eating anything they can successfully capture and devour.

Conservation status

An adult Chinese Mantis perched in a tree in camouflage in Maryland.

Only one Spanish species, *Apteromantis aptera*, is listed as Lower Risk/Near Threatened. With one exception (the ground mantis *Litaneutria minor* in Canada, where it is rare — though it is common in the United States), North American mantises are not included among threatened or endangered species, though species in other parts of the world are under threat from habitat destruction. The European mantis (*Mantis religiosa*) is the state insect of Connecticut, but the General Statutes of Connecticut do not list any special protected status, as it is a non-native species from Europe and Africa.

There is a long-standing American urban legend that killing a praying mantis is illegal and subject to a fine. The origin of this myth is unknown.

Introduced species

About 20 species are native to the United States, including the common Carolina mantis, with only one native to Canada. Two species (the Chinese mantis and the European mantis) were deliberately introduced to serve as pest control for agriculture, and have spread widely in both countries. Additionally, there is a strong market in the exotic pet trade for mantis species from Asia and Africa, and many species are bred in captivity for this purpose.

Chapter 2

Phasmatodea and Dragonfly

Phasmatodea

Phasmatodea Temporal range: 55.8–0 Ma Eocene - Recent	

Ctenomorphodes chronus

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Exopterygota
Order:	**Phasmatodea** Jacobson and Bianchi, 1902

Suborders

Agathemerodea
Timematodea
Verophasmatodea

The **Phasmatodea** (sometimes called **Phasmida**) are an order of insects, whose members are variously known as **stick insects** (in Europe and Australasia), **walking sticks** or **stick-bugs** (in the United States and Canada), **phasmids**, **ghost insects** and **leaf insects** (generally the family Phylliidae). The ordinal name is derived from the Ancient Greek *phasma*, meaning an apparition or phantom, and refers to the resemblance of many species to sticks or leaves. Their natural camouflage can make them extremely difficult to spot.

Anatomy and ecology

Phasmids can be relatively large, elongated insects. Some have cylindrical stick-like bodies, while others have a flattened, leaflike shape. The body is often further modified to resemble vegetation, with ridges resembling leaf veins, bark-like tubercles, and other forms of camouflage. A few species, such as *Carausius morosus*, are even able to change their pigmentation to match their surroundings. Many species are wingless, or have reduced wings.

The mouthparts project out from the head, and include typical chewing mandibles. All phasmids possess compound eyes, but ocelli are only found in some winged males.

The thorax is long in the winged species, where it includes the flight muscles, but is typically much shorter in the wingless forms. Where present, the first pair of wings are narrow and cornified, while the hind wings are broad, with straight longitudinal veins and multiple cross-veins. The legs are typically long and slender, and some species are capable of limb autotomy. A few species (for example those in the genus *Anisomorpha*) are capable of secreting a substance from glands on the metathorax that can cause an intense burning irritation of the eyes (and in some cases temporary blindness) and mouth of potential predators on contact.

Phasmids are herbivorous, feeding mostly on the leaves of trees and shrubs. The females, which are usually significantly larger than the males, lay their eggs individually, either sticking them to vegetation or simply depositing them on the ground. A single female may lay from 100 to 1,200 eggs after mating, depending on species. The eggs are typically camouflaged, resembling plant seeds, and may remain dormant for a full season or more before hatching. The nymphs are born already closely resembling the adults.

Taxonomy

The classification of the Phasmatodea is complex. There are many people, including amateur entomologists, studying the order, and revisions are commonplace.

The Phasmatodea were considered a suborder of Orthoptera, although most authors now consider them to form an order of their own. There is much confusion over the ordinal name, with Phasmida being preferred by many authors, although it is incorrectly formed. Phasmatodea is correctly formed, and is gaining in popularity. The term "Cheleutoptera" is now considered outdated.

They are sometimes considered related to other orders, including the Blattaria, Mantodea, Notoptera and Dermaptera, but the affiliations are uncertain and the grouping (sometimes referred to as "Orthopteroidea") may be paraphyletic and hence invalid in the traditional circumscription.

Species

There are in excess of 3,000 described species, with many more yet to be described, both in museum collections, and in the wild. The order has a worldwide distribution, but most species are found in the tropics. These tropic species vary from stick like species to those resembling bark, leaves and even lichens.

Behaviour

Stick insects, like praying mantis, show rocking behaviour in which the insect makes rhythmic, repetitive side-to-side movements. Functions proposed for this behaviour include the enhancement of crypsis by means of the resemblance to vegetation moving in the wind. However the repetitive swaying movements may be most important in allowing the insects to discriminate objects from the background by their relative movement, a visual mechanism typical of simpler animals. Rocking movements by these generally sedentary insects may replace flying or running as a source of relative motion of objects in the visual field.

Some species of phasmid are able to produce a defensive spray when threatened. The spray contains pungent-smelling volatile metabolites which it is thought the insect concentrates from its food plant. The spray from one species, *Megacrania nigrosulfurea*, is even used as a treatment for skin infections by a tribe in Papua New Guinea by virtue of its antibacterial constituents.

Stick insects as pets

Many stick insects are easy to care for, and make good pets. Almost 300 species have been reared in captivity.

The most commonly kept, the Indian (or Laboratory) stick insect, *Carausius morosus*, requires a tall (25+ cm) vivarium (even a jar with a few holes punched in the top), some bramble, ivy, privet and lettuce and an atmosphere at room temperature. Indian stick insects are almost all female with only a few half-males (gynandromorphs) and these are not needed for reproduction. They reproduce by parthenogenesis and seem content living on their own. All stick insects moult and may eat the shed skin. By the sixth moult the Indian stick insect will lay eggs.

Many of the other species of phasmids kept in captivity will feed on bramble. However, some are very specialist feeders and are therefore more difficult to rear. Beginners often make the mistake of thinking all species will feed on privet (the plant most commonly used to feed the Indian stick insect), in fact few species feed on privet. Most of the privet feeders on the Phasmid Study Group's culture list belong to the family Pseudophasmatidae and are from South America, several of these will also feed on hebe. The few members of the family Aschiphasmatidae that have been reared have to be fed on fuchsia, willow herb, or evening primrose. Some of the species in the subfamily Necrosciinae will only feed on hypericum.

Notable species

One Australian species, the Lord Howe Island stick insect, is now listed as critically endangered. It was believed extinct until its rediscovery on the rock known as Ball's Pyramid. There is a large effort in Australia to rear this species in captivity.

Females of the genus *Phobaeticus* are the world's longest insects, measuring up to 33 centimetres (13 in) from head to tip of abdomen.

Adult female *Heteropteryx dilatata* are likely to weigh up to 65 grams (2.3 oz), and captive bred specimens have been known to weigh in the order of 50 grams (1.8 oz).

The best known of the stick insects is the Indian or Laboratory stick insect (*Carausius morosus*). These insects grow to roughly 10 centimetres (3.9 in). They reproduce parthenogenically and males are unrecorded, although part male part female gynandromorphs are relatively common.

Dragonfly

Dragonfly	
	
Yellow-winged Darter	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Odonata
Suborder:	Epiprocta
Infraorder:	**Anisoptera** Selys, 1854
Families	

- Aeshnidae
- Austropetaliidae
- Chlorogomphidae
- Cordulegastridae
- Corduliidae
- Gomphidae
- Libellulidae
- Macromiidae
- Neopetaliidae
- Petaluridae
- Synthemistidae

A **dragonfly** is an insect belonging to the order Odonata, the suborder Epiprocta or, in the strict sense, the infraorder **Anisoptera**. It is characterized by large multifaceted eyes, two pairs of strong transparent wings, and an elongated body. Dragonflies are similar to damselflies, but the adults can be differentiated by the fact that the wings of most dragonflies are held away from, and perpendicular to, the body when at rest. Dragonflies possess six legs (like any other insect), but most of them cannot walk well. Dragonflies are some of the fastest insects in the world.

Dragonflies are valuable predators that eat mosquitoes, and other small insects like flies, bees, ants, and very rarely butterflies. They are usually found around lakes, ponds, streams and wetlands because their larvae, known as "nymphs", are aquatic.

Classification (Anisozygoptera)

Formerly, the Anisoptera were given suborder rank beside the "ancient dragonflies" (Anisozygoptera) which were believed to contain the two living species of the genus *Epiophlebia* and numerous fossil ones. More recently it turned out that the "anisozygopterans" form a paraphyletic assemblage of morphologically primitive relatives of the Anisoptera. Thus, the Anisoptera (true dragonflies) are reduced to an infraorder in the new suborder Epiprocta (dragonflies in general). The artificial grouping Anisozygoptera is disbanded, its members being largely recognized as extinct offshoots at various stages of dragonfly evolution. The two living species formerly placed there — the Asian relict dragonflies — form the infraorder Epiophlebioptera alongside Anisoptera.

Flight speed

Tillyard claimed to have recorded the Southern Giant Darner flying at nearly 60 miles per hour (97 km/h) in a rough field measurement. However, the greatest reliable flight speed records are for other types of insects. In general, large dragonflies like the hawkers have a maximum speed of 10–15 metres per second (22–34 mph) with average cruising speed of about 4.5 metres per second (10 mph).

Dragonflies and damselflies

Common Bluetail Damselfly

Damselflies (suborder Zygoptera), typically being smaller than dragonflies, are sometimes confused with newly moulted dragonflies. However, once a dragonfly moults, it is already fully grown. There are other distinctions that set them apart: most damselflies hold their wings at rest together above the torso or held slightly open above (such as in the family Lestidae), whereas most dragonflies at rest hold their wings perpendicular to their body, horizontally or occasionally slightly down and forward. Also, the back wing of the dragonfly broadens near the base, caudal to the connecting point at the body, while the back wing of the damselfly is similar to the front wing. The eyes on a damselfly are apart; in most dragonflies the eyes touch. Notable exceptions are the Petaluridae (Petaltails) and the Gomphidae (Clubtails).

The largest living odonate by wingspan is actually a damselfly from South America, *Megaloprepus caerulatus* (Drury, 1782) while the second largest are females of the dragonfly *Tetracanthagyna plagiata* (Wilson, 2009). The female *T. plagiata* is probably the heaviest living odonate.

Common species

Northern hemisphere

Broad-bodied Chaser

- Emperor, *Anax imperator*
- Keeled Skimmer, *Orthetrum coerulescens*
- Black-tailed Skimmer, *Orthetrum cancellatum*
- Common Whitetail, *Libellula lydia*
- Migrant Hawker, *Aeshna mixta*
- Azure Hawker, *Aeshna caerulea*
- Southern Hawker, *Aeshna cyanea*
- Norfolk Hawker, *Aeshna isosceles*
- Common Hawker, *Aeshna juncea*
- Red-veined Darter, *Sympetrum fonscolombii*
- Common Darter, *Sympetrum striolatum*
- Yellow-winged Darter, *Sympetrum flaveolum*
- Broad-bodied Chaser, *Libellula depressa*
- Four-spotted Chaser, *Libellula quadrimaculata*
- Scarce Chaser, *Libellula fulva*
- Green Darner, *Anax junius*
- Downy Emerald, *Cordulia aenea*
- Blue-eyed Darner, *Aeshna multicolor*
- Roseate Skimmer, *Orthemis ferruginea*
- Widow Skimmer, *Libellula luctuosa*
- Great Pondhawk, *Erythemis*

- Vagrant Darter, *Sympetrum vulgatum*
- *vesiculosa*
- Comet Darner, *Anax longipes*
- Banded Pennant, *Celithemis fasciata*
- Texas Emerald, *Somatochlora margarita*

Southern hemisphere

A Tau Emerald (Hemicordulia tau) in mid flight

Kirby's Dropwing (*Trithemis kirbyi*) in Tsumeb, Namibia.

Flame Skimmer

- Glistening Demoiselle *Phaon iridipennis*
- Dancing Jewel *Platycypha caligata*
- Mountain Malachite *Chlorolestes fasciatus*
- Common Spreadwing *Lestes plagiatus*
- Common Threadtail *Elattoneura glauca*
- Goldtail *Allocnemis leucosticta*
- Swamp Bluet *Africallagma glaucum*
- Pinhey's Whisp *Agriocnemis pinheyi*
- Black-tailed Bluet *Azuragrion nigridorsum*
- Common Citril *Ceriagrion glabrum*
- Yellow-faced Sprite *Pseudagrion citricola*
- Gambel's Sprite *Pseudagrion gamblesi*
- Hagen's Sprite *Pseudagrion hageni*
- Hamon's Sprite *Pseudagrion hamoni*
- Kersten's Sprite *Pseudagrion kersteni*
- Masai Sprite *Pseudagrion massaicum*
- Powdered Sprite *Pseudagrion spernatum*
- Orange Emperor *Anax speratus*
- Common Thorntail *Ceratogomphus pictus*
- Southern Yellowjack *Notogomphus praetorius*

- Ivory Pintail *Acisoma trifidum*
- Banded Groundling *Brachythemis leucosticta*
- Broad Scarlet *Crocothemis erythraea*
- Little Scarlet *Crocothemis sanguinolenta*
- Black Percher *Diplacodes lefebvrii*
- Black-tailed False-skimmer *Nesciothemis farinosa*
- Two-striped Skimmer *Orthetrum caffrum*
- Epaulet Skimmer *Orthetrum chrysostigma*
- Julia Skimmer *Orthetrum julia*
- Navy Dropwing *Trithemis furva*
- Kirby's Dropwing *Trithemis kirbyi*
- Jaunty Dropwing *Trithemis stictica*

Dragonflies in cultures

In Europe, dragonflies have often been seen as sinister. Some English vernacular names, such as "devil's darning needle" and "ear cutter", link them with evil or injury. A Romanian folk tale says that the dragonfly was once a horse possessed by the devil. Swedish folklore holds that the devil uses dragonflies to weigh people's souls. The Norwegian name for dragonflies is "Øyenstikker", which literally means *Eye Poker* and in Portugal they are sometimes called "Tira-olhos" (*Eye snatcher*). They are often associated with snakes, as in the Welsh name *gwas-y-neidr*, "adder's servant". The Southern United States term "snake doctor" refers to a folk belief that dragonflies follow snakes around and stitch them back together if they are injured.

Dragonfly symbol on a Hopi bowl from Sikyatki archaeological site.

For some Native American tribes they represent swiftness and activity, and for the Navajo they symbolize pure water. Dragonflies are a common motif in Zuni pottery; stylized as a double-barred cross, they appear in Hopi rock art and on Pueblo necklaces.

They also have traditional uses as medicine in Japan and China. In some parts of the world they are a food source, eaten either as adults or larvae; in Indonesia, for example, they are caught on poles made sticky with birdlime, then fried in oil as a delicacy.

In the United States dragonflies and damselflies are sought out as a hobby similar to birding and butterflying, known as oding, from the dragonfly's Latin species name, *odonata*. Oding is especially popular in Texas, where 225 different species of odonates have been observed. With care, with dry fingers, though it is not encouraged, dragonflies can be handled and released by oders, as can be done with butterflies.

Images of dragonflies are common in Art Nouveau, especially in jewelry designs. They also appear in posters by modern artists such as Maeve Harris. They have also been used as a decorative motif on fabrics and home furnishings.

Japan

As a seasonal symbol in Japan, the dragonfly is associated with early and late summer and early autumn.

More generally, in Japan dragonflies are symbols of courage, strength, and happiness, and they often appear in art and literature, especially haiku. The love for dragonflies is reflected in the fact that there are traditional names for almost all of the 200 species of dragonflies found in and around Japan. Japanese children catch large dragonflies as a game, using a hair with a small pebble tied to each end, which they throw into the air. The dragonfly mistakes the pebbles for prey, gets tangled in the hair, and is dragged to the ground by the weight.

As it symbolizes courage, boys are given the name of "Tonbo", meaning dragonfly. The shape of the archipelago of Japan, as seen on a map, is said to be that of a dragonfly. Hence the leading male character in Kiki's Delivery Service, in a non-Japanese setting, is named "Tonbo" so that the Japanese audience can identify with him.

Beyond this one of Japan's former names – あきつしま *(Akitsushima)* – is literally an archaic form of Dragonfly Island(s). This is attributed to a legend in which Japan's mythical founder, Emperor Jinmu, was bitten by a mosquito, which was then promptly eaten by a dragonfly.

Chapter 3

Beetle

Beetle
Temporal range: 318–0 Ma
Pennsylvanian – Recent

Collage of species of Coleoptera circumposed on a white background. from top left to bottom right, female Golden stag beetle (*Lamprima aurata*), Rhinoceros beetle (*Xylotrupes gideon*), a species of Amblytelus , Cowboy beetle (*Chondropyga dorsalis*), and a Long nose weevil (*Rhinotia hemistictus*).

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Subclass:	Pterygota
Infraclass:	Neoptera
Superorder:	Endopterygota

Order:	**Coleoptera** Linnaeus, 1758

Suborders

- Adephaga
- Archostemata
- Myxophaga
- Polyphaga

Coleoptera is an order of insects; from Greek κολεός, *koleos*, "sheath"; and πτερόν, *pteron*, "wing", thus "sheathed wing"), which contains more species than any other order in the animal kingdom, constituting almost 25% of all known life-forms. About 40% of all described insect species are beetles (about 400,000 species), and new species are discovered frequently. Some estimates put the total number of species, described and undescribed, at as high as 100 million, but 1 million is a more likely figure. The largest taxonomic family, the Curculionidae (the weevils or snout beetles), also belongs to this order.

The diversity of beetles is very wide-ranging. Being found in almost all habitats, but are not known to occur in the sea or in the polar regions. They interact with their ecosystems in several ways. They often feed on plants and fungi, break down animal and plant debris, and eat other invertebrates. Some species are prey of various animals including birds and mammals. Certain species are agricultural pests, such as the Colorado potato beetle *Leptinotarsa decemlineata*, the boll weevil *Anthonomus grandis*, the red flour beetle *Tribolium castaneum*, and the mungbean or cowpea beetle *Callosobruchus maculatus*, while other species of beetles are important controls of agricultural pests. For example, beetles in the family Coccinellidae ("ladybirds" or "ladybugs") consume aphids, scale insects, thrips, and other plant-sucking insects that damage crops.

Species in the order Coleoptera are generally characterized by a particularly hard exoskeleton and hard forewings (elytra). This elytra separates it from most other insect species, except for a few Hemiptera species. The beetle's exoskeleton is made up of numerous plates called sclerites, separated by thin sutures. This design creates the armored defenses of the beetle while maintaining flexibility. The general anatomy of a beetle is quite uniform, although specific organs and appendages may vary greatly in appearance and function between the many families in the order. Like all insects, beetles' bodies are divided into three sections: the head, the thorax, and the abdomen. The internal morphology is like other insects, however some factors are unique. Such as species of diving beetles, who use air bubbles in order to dive under the water, which could last a respectable period of time due to passive diffusion allowing oxygen to transfer from the water into the bubble.

Beetles are endopterygotes, which means that they undergo complete metamorphosis, a biological process by which an animal physically develops after birth or hatching, undergoing a series of conspicuous and relatively abrupt change in the its body structure.

Coleopteran species have an extremely intricate behavior when mating, using such methods as pheromones for communication to locate potential mates. Males may fight for females using very elongated mandibles, causing a strong divergence between males and females in sexual dimorphism.

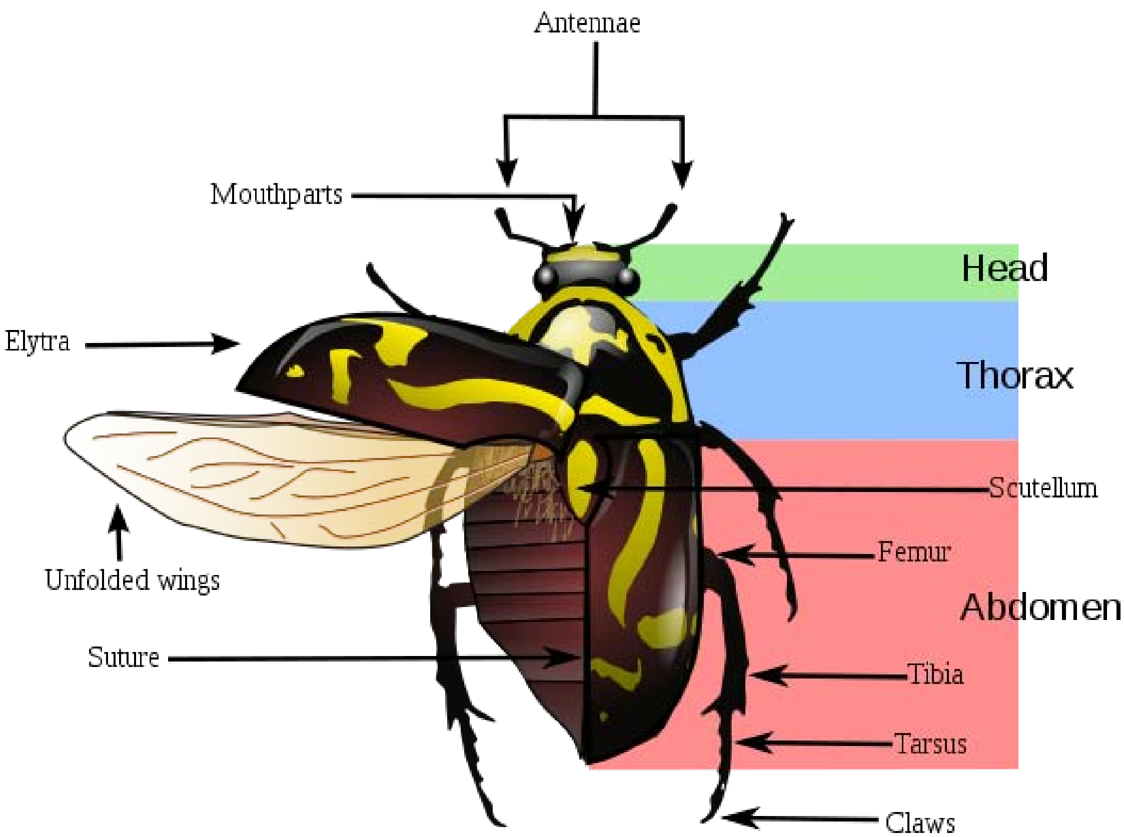
Etymology

Coleoptera comes from the Greek koleopteros, literally "sheath-wing," from "koleos" meaning "sheath," and pteron, meaning "wing. The name "Coleoptera" was given by Aristotle for the elytra, a hardened shield-like forewing. According to common vernacular, species of Coleoptera may go by an array of names, including fireflies, june bug, ladybugs, weevils, and the obvious beetles. The word beetle comes from the Old English word bitela, literally meaning small biter, deriving from the word bitel, which means biting.

Distribution and diversity

With one of the largest order of insects, with 350,000 - 400,000, including 24,000 in North America, and 20,000 in Australia, species described in four suborders (Adephaga, Archostemata, Myxophaga, and Polyphaga), which makes up about 40% of all insect species described. Even though at the family level of classification is a bit unstable, there are about 500 recognized families and subfamilies. Species of coleoptera are found in an array of natural habitats, including nearly all of them. Including water and marine habitats, and every habitat with vegetative foliage, from trees and there bark to flower, leaves and underground near roots. even being found inside the plants in galls in ever plant tissue including dead or decaying ones.

External Morphology



The morphology of a beetle, with a fiddler beetle as an example species.

Beetles are generally characterized by a particularly hard exoskeleton and hard forewings (elytra). The beetle's exoskeleton is made up of numerous plates called sclerites, separated by thin sutures. This design creates the armored defenses of the beetle while maintaining flexibility. The general anatomy of a beetle is quite uniform, although specific organs and appendages may vary greatly in appearance and function between the many families in the order. Like all insects, beetles' bodies are divided into three sections: the head, the thorax, and the abdomen.

Scarabaeus viettei (syn. *Madateuchus viettei*, Scarabaeidae) showing a "shovel head" adaptation.

Head of *Cephalota circumdata*, showing the compound eyes and mouthparts

Head

The head, having a projecting forward mouthparts or sometimes downturned, is usually heavily sclerotized and varying in size. The eyes are compound and may display remarkable adaptability, as in the case of whirligig beetles (family Gyrinidae), in which the eyes are split to allow a view both above and below the waterline. Other species also have divided eyes – some longhorn beetles (family Cerambycidae) and weevils – while many beetles have eyes that are notched to some degree. A few beetle genera also possess ocelli, which are small, simple eyes usually situated farther back on the head (on the vertexes).

Beetles' antennae are primarily organs of smell, but may also be used to feel out a beetle's environment physically. They may also be used in some families during mating, or among a few beetles for defence. Antennae vary greatly in form within the Coleoptera, but are often similar within any given family. In some cases, males and females of the same species will have different antennal forms. Antennae may be clavate (flabellate and lamellate are sub-forms of clavate, or clubbed antennae), filiform, geniculate, moniliform, pectinate, or serrate.

Beetles have mouthparts similar to those of grasshoppers. Of these parts, the most commonly known are probably the mandibles, which appear as large pincers on the front of some beetles. The mandibles are a pair of hard, often tooth-like structures that move horizontally to grasp, crush, or cut food or enemies. Two pairs of finger-like appendages are found around the mouth in most beetles, serving to move food into the mouth. These are the maxillary and labial palpi. In many species the mandibles are sexually dismorphic, with the males having theirs enlarged, with some being enormosly enlarged compared to the females of the same species.

Thorax

The thorax is segmented into the two discernible parts, the pro- and pterathorax. The pterathorax is the fused meso- and metathorax, which are commonly separate in other insect species, although being flexibly articulate from the prothorax. When viewed from below, the thorax is that part from which all three pairs of legs and both pairs of wings arise. The abdomen is everything posterior to the thorax. When viewed from above, most beetles appear to have three clear sections, but this is deceptive: on the beetle's upper surface, the middle "section" is a hard plate called the pronotum, which is only the front part of the thorax; the back part of the thorax is concealed by the beetle's wings. This further segmentation is usually best seen on the abdomen.

Acilius sulcatus, a diving beetle showing hind legs adapted for life in water

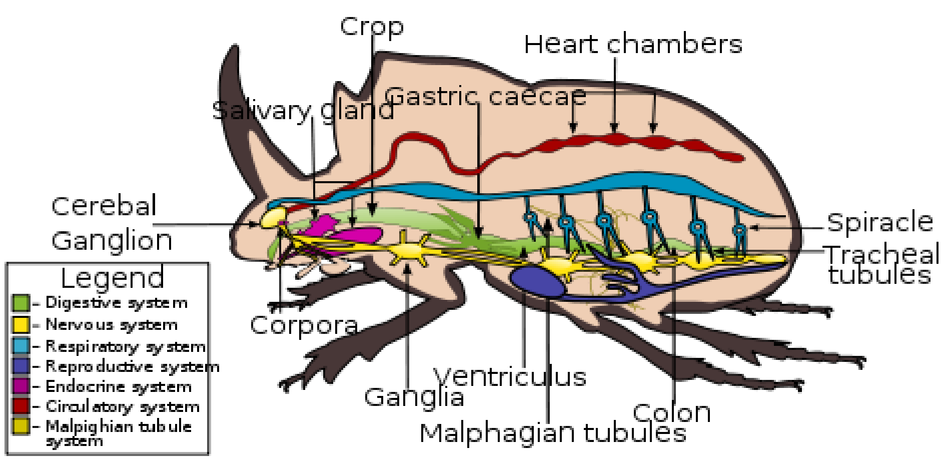
The legs, which are multi-segmented, end in two to five small segments called tarsi. Like many other insect orders beetles bear claws, usually one pair, on the end of the last tarsal segment of each leg. While most beetles use their legs for walking, legs may be variously modified and adapted for other uses. Among aquatic families – Dytiscidae, Haliplidae, many species of Hydrophilidae and others – the legs, most notably the last pair, are modified for swimming and often bear rows of long hairs to aid this purpose. Other beetles have fossorial legs that are widened and often spined for digging. Species with such adaptations are found among the scarabs, ground beetles, and clown beetles (family Histeridae). The hind legs of some beetles, such as flea beetles (within Chrysomelidae) and flea weevils (within Curculionidae), are enlarged and designed for jumping.

The elytra is connected to the pterathorax; being called as such because it is where the wings are connected (*pteron* meaning "wing" in Greek). The elytra are not used for flight, but tend to cover the hind part of the body and protect the second pair of wings (*alae*). The elytra must be raised in order to move the hind flight wings. A beetle's flight wings are crossed with veins and are folded after landing, often along these veins, and are stored below the elytra. In some beetles, the ability to fly has been lost. These include some ground beetles (family Carabidae) and some "true weevils" (family Curculionidae), but also some desert and cave-dwelling species of other families. Many of these species have the two elytra fused together, forming a solid shield over the abdomen. In a few families, both the ability to fly and the elytra have been lost, with the best known example being the glow-worms of the family Phengodidae, in which the females are larviform throughout their lives.

Abdomen

The abdomen is the section behind the metathorax, made up of a series of ring, each with a hole for breathing and respiration, called spiracles; composing three different segmented sclerites: the tergum, pleura, and the sternum. The tergum in almost all species is membranous, or usually soft and concealed by the wings and elytra when not in flight. The pleura (singular: pleuron) are usually small or hidden in some species, with each pleuron having a single spiracle. The sternum is the most widely visible part of the abdomen, being a more or less scelortized segment. The abdomen itself does not have any appendages, however some species (e.g., *Mordellidae*) have articulating sternal lobes.

Internal Morphology



A diagram showing the general internal anatomy of species of coleoptera.

The digestive system of beetles is primarily based on plants which they for the most part feed upon, with mostly the anterior midgut performing digestion. Although, in predatory species (e.g., Carabidae) most digestion occurs in the crop by means of midgut enzymes. In Elateridae species, the predatory larvae defecate enzymes on their prey, with digestion being extraorally. The alimentary canal basically comprises of a short narrow pharynx, a widened expansion, the crop and a poorly developed gizzard. After there is a midgut, that varies in dimensions between species, with a large amount of cecum, with a hingut, with varying lengths. There are typically four to six Malpighian tubules.

The nervous system in beetles contains all the types found in insects, varying between different species. With three thoracic and seven or eight abdominal ganglia can be distinguished to that in which all the thoracic and abdominal ganglia are fused to form a composite structure. Oxygen is obtained via a tracheal system. Air enters a series of tubes along the body through openings called spiracles, and is then taken into increasingly finer fibers. Pumping movements of the body force the air through the system. Beetles have hemolymph instead of blood like other insect species, the open circulatory system of the beetle is driven by a tube-like heart attached to the top inside of the thorax. Some species of diving beetles (**Dytiscidae**) carry a bubble of air with them whenever they dive beneath the water surface. This bubble may be held under the elytra or it may be trapped against the body using specialized hairs. The bubble usually covers one or more spiracles so the insect can breathe air from the bubble while submerged. An air bubble provides an insect with only a short-term supply of oxygen, but thanks to its unique physical properties, oxygen will diffuse into the bubble and displacing the nitrogen, called passive diffusion, however the volume of the bubble eventually diminishes and the beetle will have to return to the surface.

Specialized organs

Different glands specialize for different pheromones produced for finding mates. Pheromones from species of Rutelinea are produced from epithelial cells lining the inner surface of the apical abdominal segments or amino acid based pheromones of Melolonthinae from eversible glands on the abdominal apex. Other species produce different types of pheromones. Dermestids produce esters, and species of Elateridae produce fatty-acid-derived aldehydes and acetates. For means of finding a mate also, fireflies (Lampyridae) utilized modified fat body cells woth transparent surfaces backed with reflective uric acid crystals to biosynthetically produce light, or bioluminescence. The light produce is highly efficient, as it is produced by oxidation of luciferin by the enzymes luciferase in the presence of ATP (adenosine triphospate) and oxygen, producing oxyluciferin, carbon dioxide, and light.

A notable number of species have developed special glands that produce chemicals for deterring predators. The Ground beetle's (of Carabidae) defensive glands, located at the posterior, produce a variety of hydrocarbons, aldehydes, phenols, quinones, esters, and acids released from an opening at the end of the abdomen. While african carabid beetles (e.g., *Anthia* and *Thermophilium*) employ the same chemicals as ants: formic acid. While Bombardier beetles have well developed, like other carabid beetles, pygidial glands that empty from the lateral edges of the intersegment membranes between the seventh and eighth abdominal segments. The gland is made of two containing chambers. The first holds hydroquinones and hydrogen peroxide, with the second holding just hydrogen peroxide plus catalases. These chemicals mix and result in an explosive ejection, forming temperatures of around 100 C, with the brake down of hydroquinone to $H_2 + O_2 +$ quinone, with the O_2 propelling the excretion.

Tympanal organs or hearing organs, which is a membrane (tympanum) stretched across a frame backed by an air sac and associated sensory neurons, are described in two families. Several species of the genus *Cicindela* (**Cicindelidae**) have ears on the dorsal surface of the first abdominal segment beneath the wing; two tribes tribes in the family Dynastinae (**Scarabaeidae**) have ears just beneath the pronotal shield or neck membrane. The ears of both families are to ultrasonic frequencies, with strong evidence that they function to detect the presence of bats via there ultrasonic echolocation. Even though beetles constitute a large order and live in a variety of niches, examples of hearing is surprisingly lacking in species, though it is likely that most are just undiscovered.

Reproduction and development

Beetles are members of Endopterygota, which means like most other insects under complete metamorphosis, which consists of four main stages: the egg, the larva, the pupa, and the imago or adult. The larvae are commonly called grubs and the pupa are called cocoons.

Mating

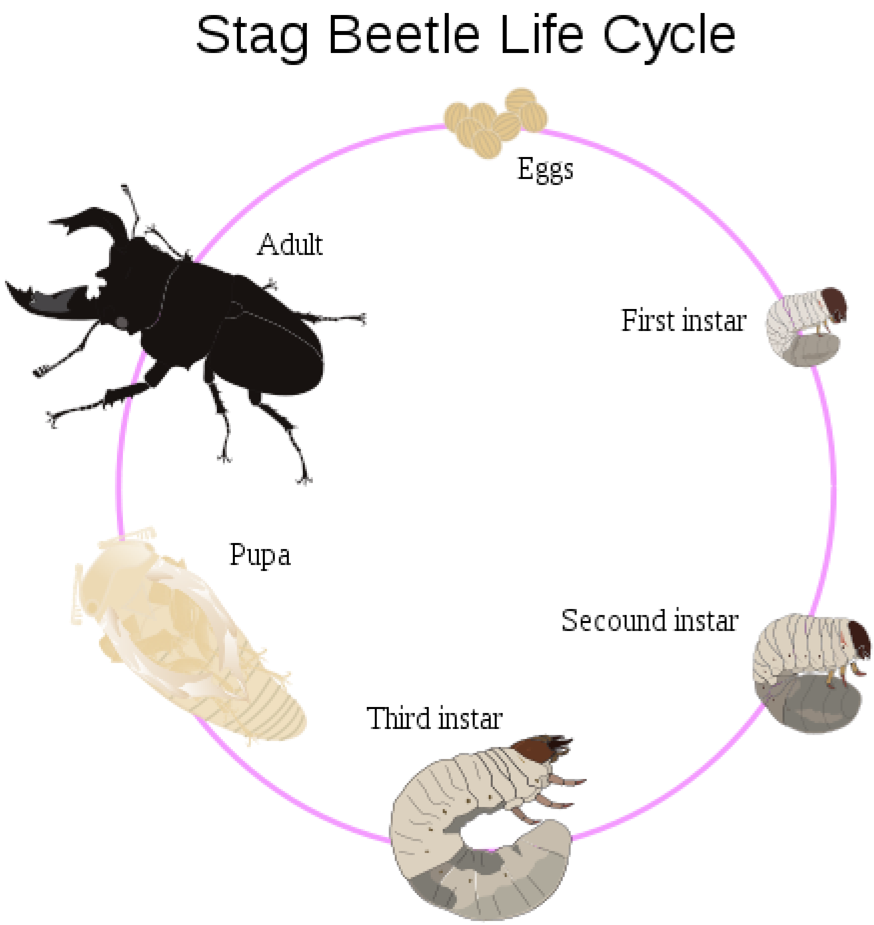
Punctate flower chafers (*Neorrhina punctata*, Scarabaeidae) mating

Beetles may display extremely intricate behavior when mating. Pheromone communication is likely to be important in the location of a mate. Different species use different chemicals for their pheromones. Some scarab beetles (e.g., Rutelinae) utilize pheromones derived from fatty acid synthesis, while other scarab beetles use amino acids and terpenoid compounds (e.g., Melolonthinae). Another way species of Coleoptera find mates is the use of biosynthesized light, or bioluminescence. This special form of a mating call is confined to fireflies (**Lampyridae**) by the use of abdominal light producing organs. The males and females engage in complex dialogue before mating, identifying different species by differences in duration, flight patterns, composition, and intensity.

Before mating male ans females may engage in various forms of behavior. Males and females may stridulate, or vibrate the object they are on. In some species (e.g., Meloidae) the male climbs onto the dorsum of the female and stroke his antennae on her head, palps and antennae. In the genus Eupompha of said family, the males draws the antennae alonga the longitudinal vertex on the male. They may not mate at all if they do not perform the precopulatory ritual.

Conflict can play a part in the mating rituals of species such as burying beetles (genus *Nicrophorus*) where conflicts between males and females rage until only one of each is left, thus ensuring reproduction by the strongest and fittest. Many male beetles are territorial and will fiercely defend their small patch of territory from intruding males. In such species, the males may often have horns on the head and/or thorax, making their overall body lengths greater than those of the females, unlike most insects. Pairing is generally short but in some cases will last for several hours. During pairing sperm cells are transferred to the female to fertilize the egg.

Life Cycle



The life cycle of the stag beetle, including the 3 instars.

Egg

A single female may lay from several dozen to several thousand eggs during her lifetime. Eggs are usually laid according to the substrate the larva will feed on upon hatching. Among others, they can be laid loose in the substrate (e.g. flour beetle), laid in clumps on leaves (e.g. Colorado potato beetle), or individually attached (e.g. mungbean beetle and other seed borers) or buried in the medium (e.g. carrot weevil).

Parental care varies between species, ranging from the simple laying of eggs under a leaf to certain scarab beetles, which construct underground structures complete with a supply of dung to house and feed their young. Other beetles are leaf rollers, biting sections of leaves to cause them to curl inwards, then laying their eggs, thus protected, inside.

Larva

A scarabaeiform larvae known as a Curl grub.

The larva is usually the principal feeding stage of the beetle life cycle. Larvae tend to feed voraciously once they emerge from their eggs. Some feed externally on plants, such as those of certain leaf beetles, while others feed within their food sources. Examples of internal feeders are most Buprestidae and longhorn beetles. The larvae of many beetle families are predatory like the adults (ground beetles, ladybirds, rove beetles). The larval period varies between species but can be as long as several years. The larva are highly varied amongst species, with a well developed and sclerotized head and have distinguishable thoracic and abdominal segments (usually the tenth, though sometimes the eight or ninth).

Beetle larvae can be differentiated from other insect larvae by their hardened, often darkened head, the presence of chewing mouthparts, and spiracles along the sides of the body. Like adult beetles, the larvae are varied in appearance, particularly between beetle families. Beetles whose larvae are somewhat flattened and are highly mobile are the ground beetles, some rove beetles, and others; their larvae are described as campodeiform. Some beetle larvae resemble hardened worms with dark head capsules and minute legs. These are elateriform larvae, and are found in the click beetle (Elateridae) and darkling beetle (Tenebrionidae) families. Some elateriform larvae of click beetles are known as wireworms. Beetles in the families of the Scarabaeoidea have short, thick larvae described as scarabaeiform, but more commonly known as grubs.

All beetle larvae go through several instars, which are the developmental stages between each moult. In many species the larvae simply increase in size with each successive instar as more food is consumed. In some cases, however, more dramatic changes occur. Among certain beetle families or genera, particularly those that exhibit parasitic lifestyles, the first instar (the planidium) is highly mobile in order to search out a host, while the following instars are more sedentary and remain on or within their host. This is known as hypermetamorphosis; examples include the blister beetles (family Meloidae) and some rove beetles, particularly those of the genus *Aleochara*.

Pupa

As with all endopterygotes, beetle larvae pupate, and from this pupa emerges a fully formed, sexually mature adult beetle, or imago. Adults have an extremely variable lifespan, from weeks to years, depending on the species. In some species the pua may go through all four forms during its development, called hypermetamorphosis (e.g., Meloidae). Pupa always have no mandibles, or abecticous. In most, the appendags are not attached to the pupa, or they are exarate; with most being obtect in form.

Behavior

Locomotion

Photinus pyralis in midflight.Photinus pyralis Firefly

Aquatic beetles use several techniques for retaining air beneath the water's surface. Beetles of the family Dytiscidae hold air between the abdomen and the elytra when diving. Hydrophilidae have hairs on their under surface that retain a layer of air against their bodies. Adult crawling water beetles use both their elytra and their hind coxae (the basal segment of the back legs) in air retention, while whirligig beetles simply carry an air bubble down with them whenever they dive.

The elytra allows beetles and weevils to both fly and move through confined spaces. Doings so by folding the delicate wings under the elytra while not flying, and folding their wings out just before take off. The unfolding and folding of the wings is operated by muscles attached to the wing base; as long as the tension on the radial and cubital veins remains, the wings remain straight. In day-flying species (e.g. Buprestidae, Scarabaeidae), flight does not include large amounts of lifting of the elytra, having the metathorac wings extended under the lateral elytra margins.

Communication

Beetles have a variety of ways to communicate. Some of which include a sophisticated chemical language through the use of pheromones. From the host tree, the mountain pine beetle have many forms of communication. They can emit both an aggregative pheromone and an anti-aggregative pheramone. The aggregative pheromone attracts other beetles to the tree, and the anti-aggregative pheromone neutralizes the aggregative pheromone. This helps to avoid the harmful effects of having too many beetles on one tree competing for resources. The mountain pine beetle can also stridulate to communicate, or rub body parts together to create sound, having a “scraper” on their abdomen that they rub against a grooved surface on the underside of their left wing cover to create a sound that is not audible to humans. Once the female beetles have arrived on a suitable pine tree host, they begin to stridulate and produce aggregative pheromones to attract other unmated males and females. New females arrive and do the same as they land and bore into the tree. As the males arrive, they enter the galleries that the females have tunneled, and begin to stridulate to let the females know they have arrived, and to also warn others that the female in that gallery is taken. At this point, the female stops producing aggregative pheromones and starts producing anti-aggregative pheromone to deter more beetles from coming.

Since species of Coleoptera use environmental stimuli to communicate, they are affected by the climate. Microclimates, such as wind or temperature, can disturb the use of pheromones; wind would blow the pheromones while they ravel through the air. Stridulating can be interrupted when the stimulus is vibrated by something else.

Parental care

a dung beetle rolling dung, near the giant tomb *Sa Ena 'e Thomes*, Sardinia, Italy

Among insect, parental care is very uncommon, only found in a few species. Some beetles also display this unique social behavior. One theory states why there is parental care is that it is necessary for the survival of the larvae, protecting them from adverse environmental conditions and predators. One species, a rover beetle (*Bledius spectabilis*) displays both causes for parental care: physical and biotic environmental factors. Said species lives in salt marshes, so the eggs and/or larvae are endangered by the rising tide. The maternal beetle will patrol the eggs and larva and apply the appropriate burrowing behavior the keep them from flooding and from asphyxiating. Another advantage is that the mother protects the eggs and larvae from the predatory carabid beetles species

Dicheirotrichus gustavi and from the parasitoid wasp species *Barycnemis blediator*. Up to 15% of larvae are killed by this parasitoid wasp, being only protected by maternal beetles in their dens.

Some species of Dung beetles also display a form of parental care. Dung beetles, from which their name is derived, collect the feces, or "dung" and roll it into a ball, sometimes being up to 50 times their own wait; albeit sometimes it is also used to store food. Usually it is the male that rolls the ball, with the female hitch-hiking or simply following behind. In some cases the male and the female roll together. When a spot with soft soil is found, they stop and bury the dung ball. They will then mate underground. After the mating, both or one of them will prepare the brooding ball. When the ball is finished, the female lays eggs inside it, a form of mass provisioning. Some species do not leave after this stage, but remain to safeguard their offspring.

Mylabris pustulata (Meloidae) feeding on the petals of *Ipomoea carnea*

Feeding

Besides being abundant and varied, beetles are able to exploit the widediversity of food sources available in their many habitats. Some are omnivores, eating both plants and animals. Other beetles are highly specialized in their diet. Many species of leaf beetles, longhorn beetles, and weevils are very host specific, feeding on only a single species of plant. Ground beetles and rove beetles (family Staphylinidae), among others, are primarily carnivorous and will catch and consume many other arthropods and small prey such as earthworms and snails. While most predatory beetles are generalists, a few species have more specific prey requirements or preferences.

Decaying organic matter is a primary diet for many species. This can range from dung, which is consumed by coprophagous species such as certain scarab beetles (family Scarabaeidae), to dead animals, which are eaten by necrophagous species such as the carrion beetles (family Silphidae). Some of the beetles found within dung and carrion are in fact predatory, such as the clown beetles, preying on the larvae of coprophagous and necrophagous insects.

Ecology

Defense and predation

Beetles may be preyed upon by other insects such as robber flies

Beetles and their larvae have a variety of strategies to avoid being attacked by predators or parasitoids. These include camouflage, mimicry, toxicity, and active defense.

Camouflage involves the use of coloration or shape to blend into the surrounding environment. This sort of protective coloration is common and widespread among beetle families, especially those that feed on wood or vegetation, such as many of the leaf beetles (family Chrysomelidae) or weevils. In some of these species, sculpturing or various colored scales or hairs cause the beetle to resemble bird dung or other inedible objects. Many of those that live in sandy environments blend in with the coloration of the substrate. For example, the Giant African longhorn beetle (*Petrognatha gigas*) which resembles the mossa nd bark of the tree from which it feeds on.

Another defense that often uses color or shape to deceive potential enemies is mimicry. A number of longhorn beetles (family Cerambycidae) bear a striking resemblance to wasps, which helps them avoid predation even though the beetles are in fact harmless. This defense can be found to a lesser extent in other beetle families, such as the scarab beetles. Beetles may combine their color mimicry with behavioral mimicry, acting like the wasps they already closely resemble. Many beetle species, including ladybirds, blister beetles, and lycid beetles can secrete distasteful or toxic substances to make them unpalatable or even poisonous. These same species often exhibit aposematism, where bright or contrasting color patterns warn away potential predators, and there are, not surprisingly, a great many beetles and other insects that mimic these chemically protected species.

Clytus arietis (Cerambycidae), a wasp mimic

Chemical defense is another important defense found amongst species of Coleoptera, usually being advertised by bright colors. Others may utilize behaviors that would be done when releasing noxious chemicals (e.g., Tenebrionidae). Chemical defense may serve purposes other then just protection from vertebrates, such as protection from a wide range of microbes, and repellents. Some species release chemicals in the form of a spray with surprising accuracy, such as ground beetles (Carabidae), may spray chemicals from their abdomen to repel predators. Some species take advantage of the plants from which they feed, and sequester the chemicals from the plant that would protect it and incorporate into their own defense. African carabid beetles (e.g., *Anthia* and *Thermophilium*) employ the same chemicals sued by ants, while Bombardier beetles have a their own unique separate gland, spraying potential predators from far distances.

Large ground beetles and longhorn beetles may defend themselves using strong mandibles and/or spines or horns to forcibly persuade a predator to seek out easier prey. Many species have large protrusions from their thorax and head such as the Rhinoceros beetle, which can be used to defended themselves from predators. Many species of weevil that feed out in the open on leaves of plants react to attack by employing a "drop-off reflex." Even further, some will combine it with thanatosis, which they will close up their legs, antennae, mandibles, ect. and use their cryptic coloration to blend in with the background. Species with varied coloration do not do this as they can not camaflouge.

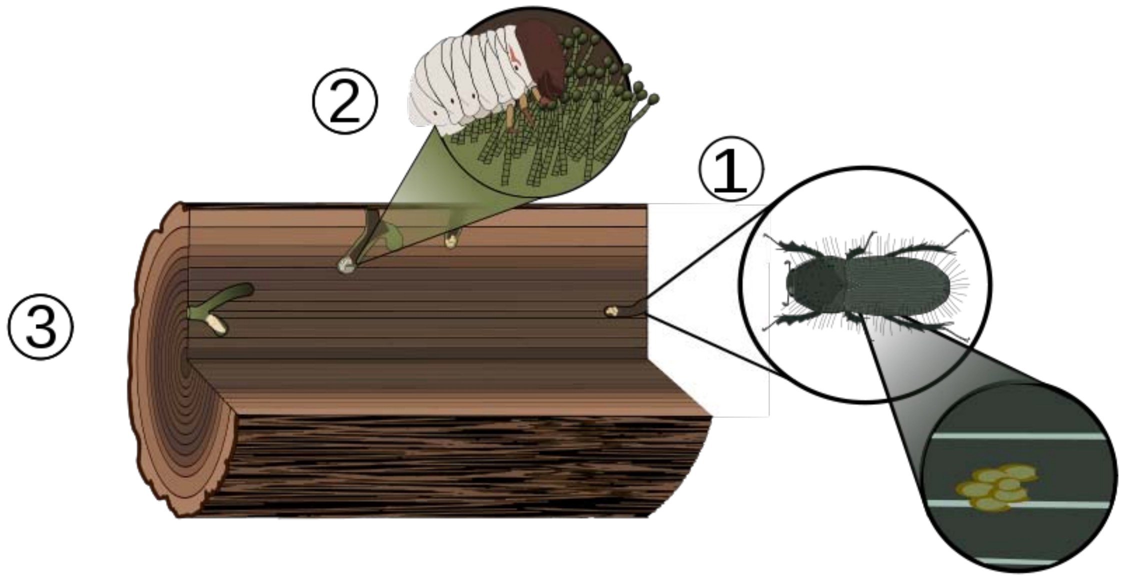
Parasitism

There are over 1000 known species of beetles to be either parasitic, predatory, or commensals in the nests of ants. Most beetle larvae can be considered parasites, as they feed on the plants and live inside the bark of trees and plants. Though there are a few species that are ectoparasitic to mammals, such as *Platypsyllus castoris*, which is affects beavers (**Castor** spp.). This beaver beetle parasite is a parasite as both an adult and a larva, with the appropriate modifications. They are wingless and eyeless with a striking dorso-ventral flattening. Additionally, P. castoris, has a remarkably modified antennal club, with antennomeres 3-11 shortened, globularly compacted, and partly enclosed in a scoop shaped antennomere 2, as is also found in **Gyrinidae** and **Dryopidae**.

other parasites include those who are parasitoids of other invertebrates, such as the small hive beetle (*Aethina tumida*) infecting Honey bee hives. The larvae tunnel through comb towards stored honey or pollen, damaging or destroying cappings and comb in the process. Larvae defecate in honey and the honey becomes discolored from the feces, which causes fermentation and a frothiness in the honey; the honey develops a characteristic odor of decaying oranges. Damage and fermentation cause honey to run out of combs, destroing large portions in hives and sometimes the extracting rooms. Heavy infestations cause bees to abscond; some beekeepers have reported the rapid collapse of even strong colonies.

Mutualism

Amongst most orders of insects, mutualism is not common, however there are some examples in species of Coleoptera. Such as the Ambrosia beetle, the Ambrosia fungus, and probably bacteria. The beetles excavate tunnels in dead trees in which they cultivate fungal gardens, their sole source of nutrition. After landing on a suitable tree, an ambrosia beetle excavates a tunnel in which it releases spores of its fungal symbiont. The fungus penetrates the plant's xylem tissue, digests it, and concentrates the nutrients on and near the surface of the beetle gallery; so the weevils and the fungus both benefit. The beetles can not eat due to toxins, which uses its relationship with fungi to help overcome it's host tree defenses and to provide nutrition for their larvae.



1: The adult beetle burrows hole into wood and lays eggs, carrying fungal spores in their mycangia
2: The larva feeds on the fungus which digest the wood, removing toxins: they mutually benefit
3: The larva pupates and then ecloses.

The beetle-fungal mutualism is chemically mediated by a bacterially produced polyunsaturated peroxide. The molecule's selective toxicity toward the beetle's fungal antagonist, combined with the prevalence and localization of its bacterial source, indicates an insect-microbe association that is both mutualistic and coevolved. This unexpected finding in a well-studied system indicates that mutualistic associations between insects and antibiotic-producing bacteria are more common than currently recognized and that identifying their small-molecule mediators can provide a powerful search strategy for therapeutically useful antimicrobial compounds.

Commensalism

Psuedoscorpions are small arachnids with a flat, pear-shaped body and pincers that resemble those of scorpions though are not, usually ranging from 2 to 8 millimetres (0.08 to 0.31 in) in length. Their small size allows them to hitch rides under the elytra of a giant harlequin beetle to be dispersed over wide areas while simultaneously being protected from predators. They may also find mating partners as other individuals join them on the beetle. This would be a form of parasitism if the beetle was harmed in the process, however the beetle is, presumably, unaffected by the presence of the hitchhikers.

Phylogeny and systematics

Baltic amber inclusions, from the Eucene era, 50 million years old (Coleoptera, Scraptiidae)

Fossil record

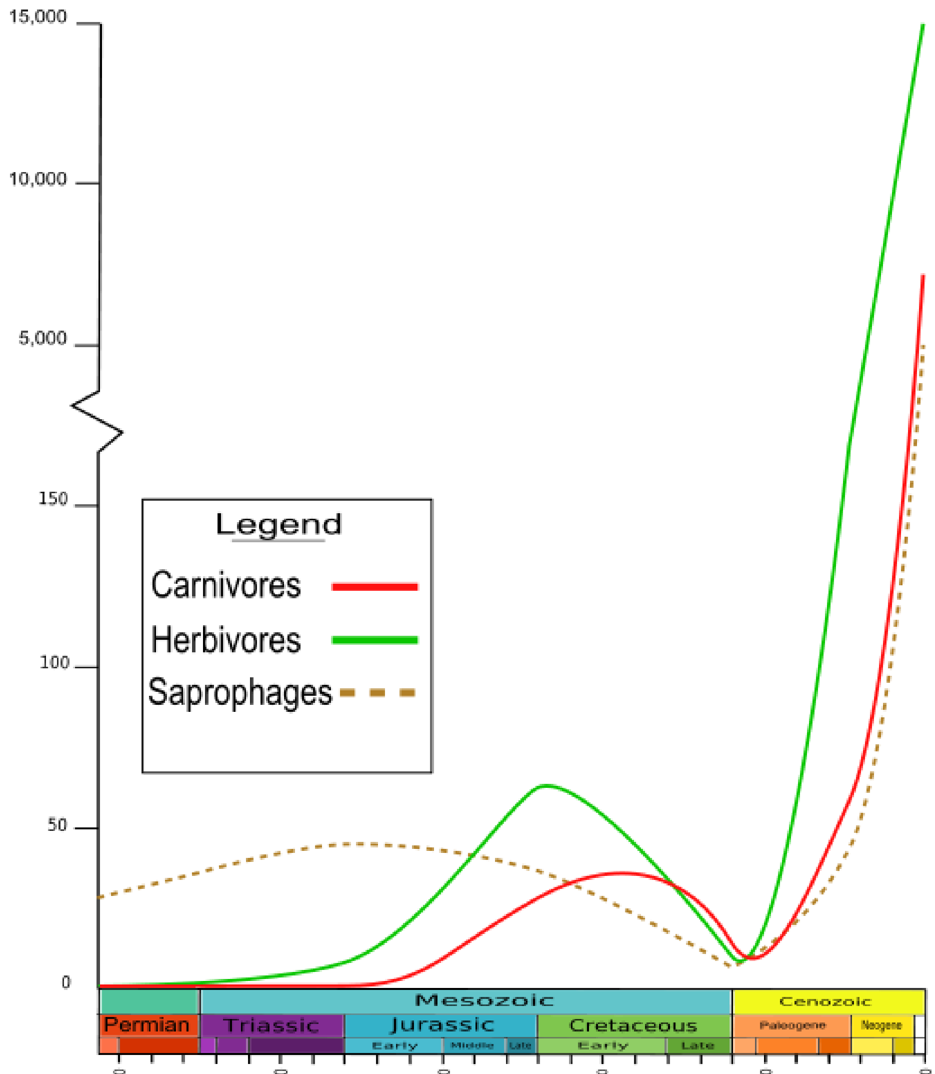
A 2007 study based on DNA of living beetles and maps of likely beetle evolution indicated that beetles may have originated during the Lower Permian, up to 299 million years ago. In 2009, a fossil beetle was described from the Pennsylvanian of Mazon Creek, Illinois, pushing the origin of the beetles to an earlier date, 318 to 299 million years ago. Fossils from this time have been found in Asia and Europe, for instance in the red slate fossil beds of Niedermoschel near Mainz, Germany. Further fossils have been found in Obora, Czechia and Tshekarda in the Ural mountains, Russia. However, there are only a few fossils from North America before the middle Permian, although both Asia and North America had been united to Euramerica. The first discoveries from North America were made in the Wellington formation of Oklahoma and were published in 2005 and 2008.

As a consequence of the P-Tr Mass Extinction at the border of Permian and Triassic, there is only little fossil record of insects including beetles from the Lower Triassic.

However, there are a few exemptions, like in Eastern Europe: At the Babiy Kamen site in the Kuznetsk Basin numerous beetle fossils were discovered, even entire specimen of the infraorders Archostemata (e.i., **Ademosynidae**, **Schizocoleidae**), Adephaga (e.i., **Triaplidae**, **Trachypachidae**) and Polyphaga (e.i., **Hydrophilidae**, **Byrrhidae**, **Elateroidea**) and in nearly a perfectly preserved condition. However, species from the families **Cupedidae** and **Schizophoroidae** are not present at this site, whereas they dominate at other fossil sites from the Lower Triassic. Further records are known from Khey-Yaga, Russia in the Korotaikha Basin. There are many important sites from the Jurassic, with more than 150 important sites with beetle fossils, the majority being situated in Eastern Europe and North Asia. In North America and especially in South America and Africa the number of sites from that time period is smaller and the sites have not been exhaustively investigated yet. Outstanding fossil sites include Solnhofen in Upper Bavaria, Germany, Karatau in South Kazakhstan, the Yixian formation in Liaoning, North China as well as the Jiulongshan formation and further fossil sites in Mongolia. In North America there are only a few sites with fossil records of insects from the Jurassic, namely the shell limestone deposits in the Hartford basin, the Deerfield basin and the Newark basin.

Fossil buprestid beetle from the Eocene Messel pit, which retains its structural color

There is a large number of important fossil sites worldwide containing beetles from the Cretaceous. Most of of them are located in Europe and Asia and belong to the temperate climate zone during the Cretaceous. A few of the fossil sites mentioned in the chapter Jurassic also shed some light on the early cretaceous beetle fauna (e.g. the Yixian formation in Liaoning, North China). Further important sites from the Lower Cretaceous include the Crato Fossil Beds in the Araripe basin in the Ceará, North Brazil as well as overlying Santana formation, with the latter was situated near the paleoequator, or the position of the earth's equator in the geologic past as defined for a specific geologic period. In Spain there are important sites near Montsec and Las Hoyas. In Australia the Koonwarra fossil beds of the Korumburra group, South Gippsland, Victoria is noteworthy. Important fossil sites from the Upper Cretaceous are Kzyl-Dzhar in South Kazakhstan and Arkagala in Russia.



The phylogenetic growth of three different trophic levels in Coleoptera by number of genera.

Evolution

The oldest known insect that resembles species of Coleoptera date back to the Lower Permian (270 mya), though they instead have 13-segmented antennae, elytra with more fully developed venation and more irregular longitudinal ribbing, and an abdomen and ovipositor extending beyond the apex of the elytra. The oldest true beetle, that is having features that include 11-segmented antennae, regular longitudinal ribbing on the elytra, and having genitalia that are internal. At the end of the Permian, the biggest mass extinction in the history history took place, collectively called the Permian–Triassic extinction event: 30% of all insect species became extinct, however, it is the only mass extinction of insects in Earth's history until today.

Consequence do to the P-Tr extinction, there is only little fossil record of insects including beetles from the Lower Triassic (220 mya). Around this time, during the Late Triassic, mycetophagous, or fungus feeding species (e.i. **Cupedidae**) appear in the fossil record. In the stages of the Upper Triassic representatives of the algophagous, or algae feeding species (e.i. **Triaplidae** and **Hydrophilidae**) begin to appear, as well as predatory water beetles. The first primitive weevils appear (e.i. **Obrienidae**), as well as the first representatives of the rove beetles (e.i. **Staphylinidae**), which show no marked difference in physique compared to recent species.

During the Jurassic (210-145 mya) there was a dramatic increase in the known diversity of family-level Coleoptera. This includes the development and growth of carnivorous and herbivorous species. Species of the superfamily **Chrysomeloidea** are believed to have developed around the same time, which include a wide array of plant host ranging from cycads and conifers, to angiosperms. Close to the Upper Jurassic, the portion of the **Cupedidae** decreased, however at the same time the diversity of the early plant eating, or phytophagous species increased. Most of the recent phytophagous species of Coleoptera feed on flowering plants or angiosperms. It is believed that the increase in diversity of the angiosperms also influenced the diversity of the phytophagous species, which doubled during the Middle Jurassic. However, recently doubts have been raised since the increase of the number of beetle families during the Cretaceous does not correlate with the increase of the number of angiosperm species. Also around the same time, numerous primitive weevils (e.i., **Curculionoidea**) and click beetles (e.i. *Elateroidea*) appeared. Also first jewel beetles (e.i., **Buprestidae**) are present, however, they were rather rare until the Cretaceous. The first scarab beetles would apear around this time, however they where not coprophagous, or feeding upon fecal matter, presumably feeding upon the rotting wood with the help of fungus, and early example of a mutualistic relationship.

The Cretaceous witness the initiation of the most recent round of southern landmass fragmentation, via the opening of the southern Atlantic ocean and the isolation of New Zealand, while the South America, Antarctica, and Australia grew more distant. During the Cretaceous the diversity of **Cupedidae** and **Archostemata** decreased considerably. Predatory ground beetles (**Carabidae**) and rove beetles (**Staphylinidae**) began to distribute into different patterns: whereas the **Carabidae** predominantly occurred in the warm regions, the **Staphylinidae** and click beetles (**Elateridae**) preferred many areas with temperate climate. Likewise, predatory species of **Cleroidea** and **Cucujoidea**, hunted their prey under the bark of trees together with the jewel beetles (**Buprestidae**). The jewel beetles diversity increased rapidly during the Cretaceous, as they were the primary consumers of wood, while longhorn beetles (**Cerambycidae**) were rather rare and their diversity increased only towards the end of the Upper Cretaceous. The first coprophagous beetles have been recorded from the Upper Cretaceous, and are believed to have lived on the excrement of herbivorous dinosaurs, however there is still a discussion, whether the beetles where always tied to mammals during its development. Also, the first species with an adaption of both larvae and adults to the aquatic lifestyle are found. Whirligig beetles (**Gyrinidae**) were moderately diverse, although other early beetles (e.i., **Dytiscidae**) where less, with the most widespread being the species of **Coptoclavidae**, which preyed on aquatic fly larvae.

The time between the Paleogene and the Neogene, or more recent history is where today's beetles developed. During this time, the continents began to situate themselves to where we see them today. Around 5 million years ago the land bridge between South America and North America was formed, and this is when fauna exchange between Asia and North America started. Even though many recent genera and species already existed during the Miocene, however, their distribution differed considerably from today's.

Phylogeny

These suborders diverged in the Permian and Triassic. Their phylogenetic relationship is uncertain, with the most popular hypothesis being that Polyphaga and Myxophaga are most closely related, with Adephaga as the sister group to those two, and Archostemata as sister to the other three collectively. Although there are six other competing hypotheses, the other most widely discussed hypothesis is Myxophaga is the sister group of all remaining beetles rather then just Polyphaga. Evidence for a close relationship of the two suborders, Polyphaga and Myxophaga, includes the shared reduction in the number of larval leg articles. further considered the Adephaga as sister to Myxophaga and Polyphaga, based on their completely sclerotized elytra, reduced number of crossveins in the hind wings, and folded (as opposed to rolled) hind wings of those three suborders.

Recent cladistic analysis of some of the structural characteristics supports the Polyphaga and 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, or as the sister group of beetles, or more distantly related to insects.

Taxonomy

There are about 450,000 species of beetles – representing about 40% of all known insects. Such a large number of species poses special problems for classification, with some families consisting of thousands of species and needing further division into subfamilies and tribes. This immense number of species allegedly led evolutionary biologist J. B. S. Haldane to quip, when some theologians asked him what could be inferred about the mind of the Creator from the works of His Creation, that God displayed "an inordinate fondness for beetles".

- Polyphaga is the largest suborder, containing more than 300,000 described species in more than 170 families, including rove beetles (Staphylinidae), scarab beetles (Scarabaeidae), blister beetles (Meloidae), stag beetles (Lucanidae) and true weevils (Curculionidae). These beetles can be identified by the cervical sclerites (hardened parts of the head used as points of attachment for muscles) absent in the other suborders.
- Adephaga contains about 10 families of largely predatory beetles, includes ground beetles (Carabidae), Dytiscidae and whirligig beetles (Gyrinidae). In these beetles, the testes are tubular and the first abdominal sternum (a plate of the exoskeleton) is divided by the hind coxae (the basal joints of the beetle's legs).
- Archostemata contains four families of mainly wood-eating beetles, including reticulated beetles (Cupedidae) and the telephone-pole beetle.
- Myxophaga contains about 100 described species in four families, mostly very small, including Hydroscaphidae and the genus *Sphaerius*.

Relationship to people

As pests

Larvae of the Colorado potato beetle, *Leptinotarsa decemlineata*

Many agricultural, forestry, and household insect pests are beetles. These include the following:

- The Colorado potato beetle, *Leptinotarsa decemlineata*, is a notorious pest of potato plants. Crops are destroyed and the beetle can only be treated by employing expensive pesticides, many of which it has begun to develop resistance to. As well as potatoes, suitable hosts can be a number of plants from the potato family (Solanaceae), such as nightshade, tomato, aubergine and capsicum.

- The boll weevil, *Anthonomus grandis*, has cost cotton producers in the United States billions of dollars since it first entered that country.
- The bark beetles *Hylurgopinus rufipes* and *Scolytus multistriatus*, the elm leaf beetle, *Pyrrhalta luteola*, and other beetles attack elm trees. The bark beetles are important elm pests because they carry Dutch elm disease as they move from infected breeding sites to feed on healthy elm trees. The spread of the fungus by the beetle has led to the devastation of elm trees in many parts of the Northern Hemisphere, notably in Europe and North America.

Red flour beetle, *Tribolium castaneum*

- Flour beetles are pests of cereal silos. They feed on wheat and other grains and are adapted to survive in very dry environments. They are a major pest in the agricultural industry and are highly resistant to insecticides.
- The death watch beetle, *Xestobium rufovillosum*, (family Anobiidae) is of considerable importance as a pest of older wooden buildings in Great Britain. It attacks hardwoods such as oak and chestnut, always where some fungal decay has taken or is taking place. It is thought that the actual introduction of the pest into buildings takes place at the time of construction.

- Coconut hispine beetle, *Brontispa longissima*, feeds on young leaves and damages seedlings and mature coconut palms. On September 27, 2007, Philippines' Metro Manila and 26 provinces were quarantined due to having been infested with this pest (to save the $800-million Philippine coconut industry).
- The mountain pine beetle normally attacks mature or weakened lodgepole pine. It can be the most destructive insect pest of mature pine forests. The current infestation in British Columbia is the largest Canada has ever seen.

As beneficial

Coccinella septempunctata, a beneficial beetle

A number of insects are beneficial to humans, usually by controlling the populations of pests.

Both the larvae and adults of some ladybugs (family Coccinellidae) are found in aphid colonies. Other ladybugs feed on scale insects and mealybugs. If normal food sources are scarce, they may feed on other things, such as small caterpillars, young plant bugs, honeydew and nectar.

Ground beetles (family Carabidae) are common predators of many different insects and other arthropods, including fly eggs, caterpillars, wireworms and others.

Plant-feeding beetles are often important beneficial insects, controlling problem weeds. Some flea beetles of the genus *Aphthona* feed on *Euphorbia esula* (leafy spurge, Euphorbiaceae), a considerable weed of rangeland in western North America.

Dung beetles (Coleoptera, Scarabidae) have been successfully used to reduce the populations of pestilent flies and parasitic worms that breed in cattle dung. The beetles make the dung unavailable to breeding pests by quickly rolling and burying it in the soil, with the added effect of improving soil fertility and nutrient cycling. The Australian Dung Beetle Project (1965–1985), led by Dr. George Bornemissza of the Commonwealth Scientific and Industrial Research Organization introduced species of dung beetle to Australia from South Africa and Europe and effectively reduced the bush fly (*Musca vetustissima*) population by 90%.

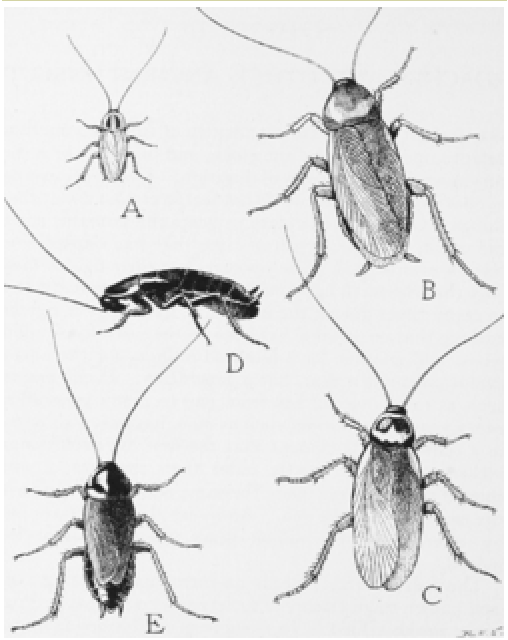
Some farmers develop beetle banks to foster and provide cover for beneficial beetles.

Some beetles of the family Dermestidae are often used in taxidermy to clean bones of remaining flesh.

Chapter 4

Cockroach

Cockroach	



Common household roaches A. German cockroach, B. American cockroach, C. Australian cockroach, D&E. Oriental cockroach (♀ & ♂)

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapodaa
Class:	Insecta
Subclass:	Pterygota
Infraclass:	Neoptera
Superorder:	Dictyoptera

Order:	**Blattodea**

Families
Blaberidae
Blattellidae
Blattidae
Cryptocercidae
Polyphagidae
Nocticolidae
Tryonicidae
Lamproblattidae

Cockroaches are insects of the order Blattaria or Blattodea. The name *cockroach* comes from the Spanish word *cucaracha*, *chafer*, *beetle*, from cuca "kind of caterpillar." The scientific name derives from the Latinized Greek name for the insect (Doric Greek: βλάττα, *blátta*; Ionic and Attic Greek: βλάττη, *bláttē*; Latin: *Blatta*).

There are about 4,500 species of cockroach, of which about 30 species are associated with human habitations and about four species are well known as pests.

Among the best-known pest species are the American cockroach, *Periplaneta americana*, which is about 30 millimetres (1.2 in) long, the German cockroach, *Blattella germanica*, about 15 millimetres (0.59 in) long, the Asian cockroach, *Blattella asahinai*, also about 15 millimetres (0.59 in) in length, and the Oriental cockroach, *Blatta orientalis*, about 25 millimetres (0.98 in). Tropical cockroaches are often much bigger, and extinct cockroach relatives and 'roachoids' such as the Carboniferous *Archimylacris* and the Permian *Apthoroblattina* were not as large as the biggest modern species. They usually live alone only coming together to mate.

Selected species

- *Blattella germanica*, German cockroach
- *Blaptica dubia*, South American/Peruvian Dubia cockroach
- *Blatta orientalis*, Oriental cockroach
- *Blattella asahinai*, Asian cockroach
- *Blaberus craniifer*, true death's head cockroach
- *Blaberus discoidalis*, discoid cockroach or false death's head
- *Eurycotis floridana*, Florida woods cockroach
- *Gromphadorhina portentosa*, Madagascar hissing cockroach
- *laxta granicollis*, Bark cockroach
- *Parcoblatta pennsylvanica*, Pennsylvania woods cockroach
- *Periplaneta americana*, American cockroach
- *Periplaneta australasiae*, Australian cockroach
- *Periplaneta brunnea*, black Mississippi cockroach
- *Periplaneta fuliginosa*, smokybrown cockroach
- *Pycnoscelus surinamensis*, Surinam cockroach

- *Supella longipalpa*, brown-banded cockroach

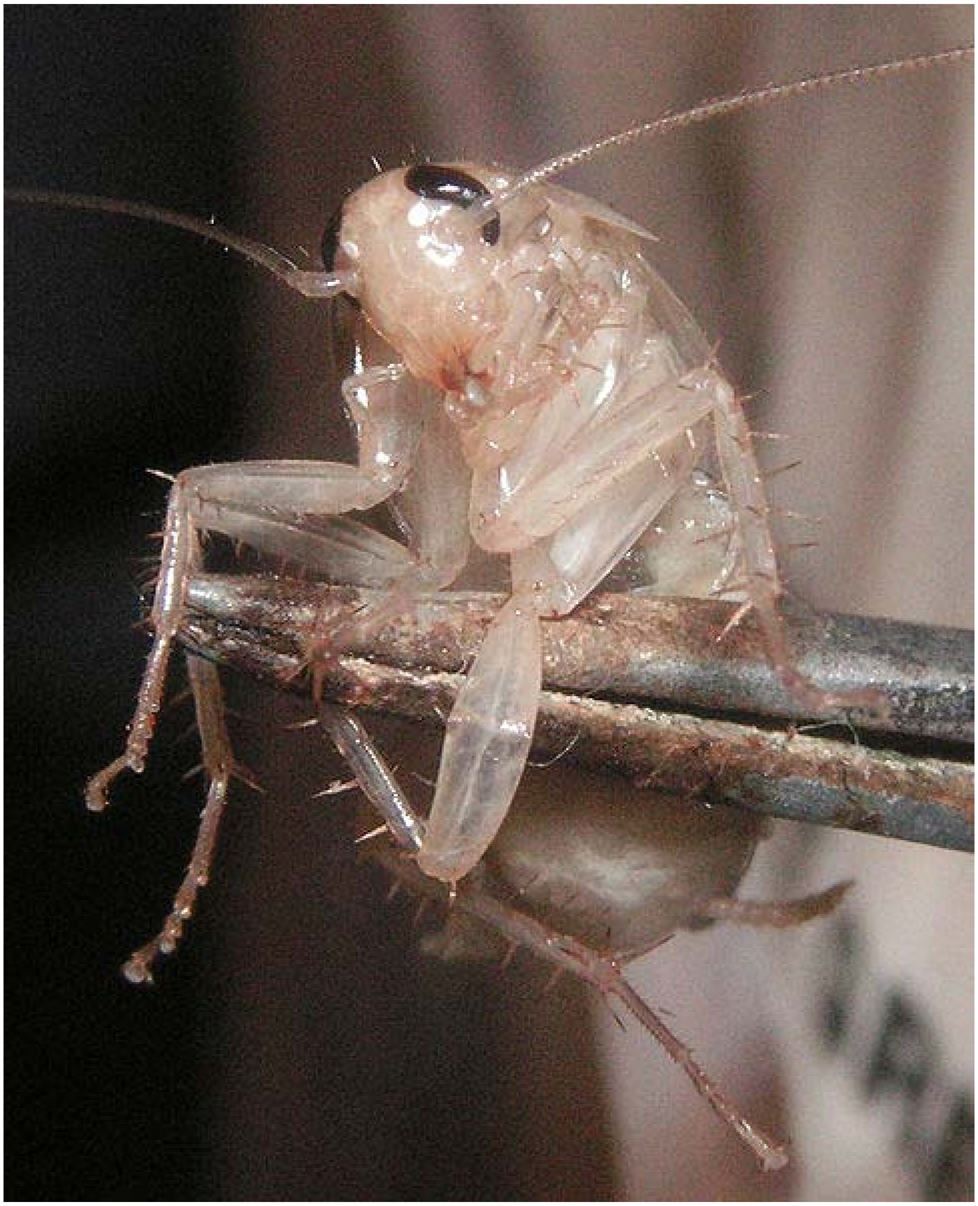
Evolutionary history and relationships

A 40-50 million year old cockroach in Baltic amber

Mantodea, Isoptera, and Blattaria are usually combined by entomologists into a higher group called Dictyoptera. Current evidence strongly suggests that termites evolved directly from true cockroaches, and many authors now consider termites to be an epifamily of cockroaches, as Blattaria excluding Isoptera is not a monophyletic group.

Historically, the name Blattaria has been used largely interchangeably with the name **Blattodea**, and this name is used for the order by the current world catalogue, the Blattodea Species File Online. Another name, **Blattoptera** has come into use for this same paraphyletic group. These earliest cockroach-like fossils ("Blattopterans" or "roachids") are from the Carboniferous period between 354–295 million years ago. However, these fossils differ from modern cockroaches in having long external ovipositors and are the ancestors of mantises as well as modern cockroaches. The first fossils of modern cockroaches with internal ovipositors appear in the early Cretaceous.

Behavior



A cockroach soon after ecdysis.

A bush cockroach (Ellipsidion australe).

Cockroaches live in a wide range of environments around the world. Pest species of cockroaches adapt readily to a variety of environments, but prefer warm conditions found within buildings. Many tropical species prefer even warmer environments and do not fare well in the average household.

The spines on the legs were earlier considered to be sensory, but observations of their locomotion on sand and wire meshes have demonstrated that they help in locomotion on difficult terrain. The structures have been used as inspiration for robotic legs.

Cockroaches leave chemical trails in their feces as well as emitting airborne pheromones for swarming and mating. These chemical trails transmit bacteria on surfaces.Other cockroaches will follow these trails to discover sources of food and water, and also discover where other cockroaches are hiding. Thus, cockroaches can exhibit emergent behavior, in which group or swarm behavior emerges from a simple set of individual interactions.

Research has shown that group-based decision-making is responsible for complex behavior such as resource allocation. In a study where 50 cockroaches were placed in a dish with three shelters with a capacity for 40 insects in each, the insects arranged themselves in two shelters with 25 insects in each, leaving the third shelter empty. When the capacity of the shelters was increased to more than 50 insects per shelter, all of the cockroaches arranged themselves in one shelter. Researchers found a balance between cooperation and competition exists in the group decision-making behavior found in cockroaches. The models used in this research can also explain the group dynamics of other insects and animals.

Cockroaches are mainly nocturnal and will run away when exposed to light. A peculiar exception is the Asian cockroach, which is attracted to light. Another study tested the hypothesis that cockroaches use just two pieces of information to decide where to go under those conditions: how dark it is and how many other cockroaches there are. The study conducted by José Halloy and colleagues at the Free University of Brussels and other European institutions created a set of tiny robots that appear to the roaches as other roaches and can thus alter the roaches' perception of critical mass. The robots were also specially scented so that they would be accepted by the real roaches.

Additionally, researchers at Tohoku University engaged in a classical conditioning experiment with cockroaches and discovered that the insects were able to associate the scent of vanilla and peppermint with a sugar treat.

Description

Cockroaches are generally rather large insects. Most species are about the size of a thumbnail, but several species are bigger. The world's heaviest cockroach is the Australian giant burrowing cockroach, which can reach 9 centimetres (3.5 in) in length and weigh more than 30 grams (1.1 oz). Comparable in size is the Central American giant cockroach *Blaberus giganteus*, which grows to a similar length but is not as heavy.

Cockroaches have a broad, flattened body and a relatively small head. They are generalized insects, with few special adaptations, and may be among the most primitive living neopteran insects. The mouthparts are on the underside of the head and include generalised chewing mandibles. They have large compound eyes, two ocelli, and long, flexible, antennae.

The first pair of wings (the tegmina) are tough and protective, lying as a shield on top of the membranous hind wings. All four wings have branching longitudinal veins, and multiple cross-veins. The legs are sturdy, with large coxae and five claws each. The abdomen has ten segments and several cerci.

Eggs and egg capsules

Female *Blatella germanica* with ootheca.

Hatched Ootheca

Female cockroaches are sometimes seen carrying egg cases on the end of their abdomen; the egg case of the German cockroach holds about 30 to 40 long, thin eggs, packed like frankfurters in the case called an *ootheca*. The eggs hatch from the combined pressure of the hatchlings gulping air. The hatchlings are initially bright white nymphs and continue inflating themselves with air, becoming harder and darker within about four hours. Their transient white stage while hatching and later while molting has led many to claim the existence of albino cockroaches.

A female German cockroach carries an egg capsule containing around 40 eggs. She drops the capsule prior to hatching, though live births do occur in rare instances. Development from eggs to adults takes 3 to 4 months. Cockroaches live up to a year. The female may produce up to eight egg cases in a lifetime; in favorable conditions, she can produce 300 to 400 offspring. Other species of cockroach, however, can produce an extremely high number of eggs in a lifetime; in some cases a female needs to be impregnated only once to be able to lay eggs for the rest of her life.

Sounds

Aside from the famous hissing noise, some cockroaches (including a species in Florida) will make a chirping noise.

Physiology

Digestive tract

Cockroaches are most common in tropical and subtropical climates. Some species are in close association with human dwellings and widely found around garbage or in the kitchen. Cockroaches are generally omnivorous with the exception of the wood-eating species such as *Cryptocercus*; these roaches are incapable of digesting cellulose themselves, but have symbiotic relationships with various protozoans and bacteria that digest the cellulose, allowing them to extract the nutrients.

The similarity of these symbionts in the genus *Cryptocercus* to those in termites are such that it has been suggested that they are more closely related to termites than to other cockroaches, and current research strongly supports this hypothesis of relationships. All species studied so far carry the obligate mutualistic endosymbiont bacterium *Blattabacterium*, with the exception of *Nocticola australiensise*, an Australian cave dwelling species without eyes, pigment or wings, and which recent genetic studies indicates are very primitive cockroaches.

Tracheae and breathing

Nymph of a cockroach, 3 mm in length.

Cockroaches, like all insects, breathe through a system of tubes called *tracheae*. The tracheae of insects are attached to the spiracles, excluding the head. Thus cockroaches, like all insects, are not dependent on the mouth and windpipe to breathe. The valves open when the CO_2 level in the insect rises to a high level; then the CO_2 diffuses out of the tracheae to the outside and fresh O_2 diffuses in. Unlike in vertebrates that depend on blood for transporting O_2 and CO_2, the tracheal system brings the air directly to cells, the tracheal tubes branching continually like a tree until their finest divisions, tracheoles, are associated with each cell, allowing gaseous oxygen to dissolve in the cytoplasm lying across the fine cuticle lining of the tracheole. CO_2 diffuses out of the cell into the tracheole.

While cockroaches do not have lungs and thus do not actively breathe in the vertebrate lung manner, in some very large species the body musculature may contract rhythmically to forcibly move air out and in the spiracles; this may be considered a form of breathing.

Reproduction

Cockroaches use pheromones to attract mates, and the males practice courtship rituals such as posturing and stridulation. Like many insects, cockroaches mate facing away from each other with their genitalia in contact, and copulation can be prolonged. A few species are known to be parthenogenetic, reproducing without the need for males.

The female usually attaches the egg-case to a substrate, inserts it into a suitably protective crevice, or carries it about until just before the eggs hatch. Some species, however, are ovoviviparous, keeping the eggs inside their bodies, with or without an egg-case, until they hatch. At least one genus, *Diploptera* is fully viviparous.

Cockroach nymphs are generally similar to the adults, except for undeveloped wings and genitalia. Development is generally slow, and may take anywhere from a few months to over a year. The adults are also long-lived, and have been recorded as surviving for four years in the laboratory.

Hardiness

Roach Leg

Cockroaches are among the hardiest insects on the planet. Some species are capable of remaining active for a month without food and are able to survive on limited resources like the glue from the back of postage stamps. Some can go without air for 45 minutes. In one experiment, cockroaches were able to recover from being submerged underwater for half an hour.

Ootheca of *Periplaneta americana*; Florianópolis, SC, Brazil.

It is popularly suggested that cockroaches will "inherit the earth" if humanity destroys itself in a nuclear war. Cockroaches do indeed have a much higher radiation resistance than vertebrates, with the lethal dose perhaps 6 to 15 times that for humans. However, they are not exceptionally radiation-resistant compared to other insects, such as the fruit fly.

The cockroach's ability to withstand radiation better than human beings can be explained through the cell cycle. Cells are most vulnerable to the effects of radiation when they are dividing. A cockroach's cells divide only once each time it molts, which is weekly at most in a juvenile roach. Since not all cockroaches would be molting at the same time, many would be unaffected by an acute burst of radiation, but lingering radioactive fallout would still be harmful.

Role as pests

Cockroaches are one of the most commonly noted household pest insects. They feed on human and pet food, and can leave an offensive odor. They can also passively transport microbes on their body surfaces including those that are potentially dangerous to humans, particularly in environments such as hospitals. Cockroaches have been shown to be linked with allergic reactions in humans. One of the proteins that triggers allergic reactions has been identified as tropomyosin. These allergens have also been found to be linked with asthma.

General preventive measures against household pests include keeping all food stored away in sealed containers, using garbage cans with a tight lid, frequent cleaning in the kitchen, and regular vacuuming. Any water leaks, such as dripping taps, should also be repaired. It is also helpful to seal off any entry points, such as holes around baseboards, in between kitchen cabinets, pipes, doors, and windows with some steel wool or copper mesh and some cement, putty or silicone caulk.

Diatomaceous earth applied as a fine powder works very well to eliminate cockroaches as long as it remains in place and dry. Diatomaceous earth is harmless to humans and feels like talcum powder. Most insects, including bed bugs, are vulnerable to it.

Some cockroaches have been known to live up to three months without food and a month without water. Frequently living outdoors, although preferring warm climates and considered "cold intolerant," they are resilient enough to survive occasional freezing temperatures. This makes them difficult to eradicate once they have infested an area.

Cockroach control, with cockroach baits, boric acid, and hydramethylnon gel.

There are numerous parasites and predators of cockroaches, but few of them have proven to be highly effective for biological control of pest species. Wasps in the family Evaniidae are perhaps the most effective insect predators, as they attack the egg cases, and wasps in the family Ampulicidae are predators on adult and nymphal cockroaches (e.g., *Ampulex compressa*). The house centipede is probably the most effective control agent of cockroaches, though many homeowners find the centipedes themselves objectionable.

Ampulex wasps sting the roach more than once and in a specific way. The first sting is directed at nerve ganglia in the cockroach's thorax; temporarily paralyzing the victim for 2–5 minutes, which is more than enough time for the wasp to deliver a second sting. The second sting is directed into a region of the cockroach's brain that controls the escape reflex, among other things. When the cockroach has recovered from the first sting, it makes no attempt to flee. The wasp clips the antennae with its mandibles and drinks some of the hemolymph before walking backwards and dragging the roach by its clipped antennae to a burrow, where an egg will be laid upon it. The wasp larva feeds on the subdued, living cockroach.

Bait stations, gels containing hydramethylnon or fipronil, as well as boric acid powder, are toxic to cockroaches. Baits with egg killers are also quite effective at reducing the cockroach population. Additionally, pest control products containing deltamethrin or pyrethrin are very effective.

In Singapore and Malaysia, taxi drivers use Pandan leaves as a cockroach repellent in their vehicles.

An inexpensive roach trap can easily be made from a deep smooth-walled jar with some roach food inside, placed with the top of the jar touching a wall or with sticks leading up to the top, so that the roaches can reach the opening. Once inside, they cannot climb back out. An inch or so of water or stale beer (by itself a roach attractant) will ensure they drown. The method works well with the American cockroach but less so with the German cockroach. A bit of Vaseline can be smeared on the inside of the jar to enhance slipperiness. The method is sometimes called the "Vegas roach trap" after it was popularized by a Las Vegas-based TV station. This version of the trap uses coffee grounds and water.

Some of the earliest writings about cockroaches encouraged their use as medicine. Pedanius Dioscorides (1st century), Abu Hanifa ad-Dainuri (9th century), and Kamal al-Din al-Damiri (14th century) all offered medicines that either suggest grinding them up with oil or boiling them.

Cockroaches are but one of many insects whose nutritional excellence has been underestimated or scorned, according to The Eat-A-Bug Cookbook, which also reports (on p.66) that Lafcadio Hearn found that many New Orleanians had great faith in a remedy of boiled cockroach tea.

Pest control is cited as one of the reasons for reduced populations of cockroaches in ex-USSR countries.

Chapter 5

Hymenoptera

Hymenoptera Temporal range: Triassic - Recent 251–0 Ma	

female *Netelia producta*

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Hymenopterida
Order:	**Hymenoptera** Linnaeus, 1758

Suborders

Apocrita
Symphyta

Hymenoptera is one of the largest orders of insects, comprising the sawflies, wasps, bees and ants. There are over 130,000 recognised species, with many more remaining to be described. The name refers to the heavy wings of the insects, and is derived from the Ancient Greek ὑμήν (hymen): membrane and πτερόν (pteron): wing. The hindwings are connected to the forewings by a series of hooks called hamuli.

Females typically have a special ovipositor for inserting eggs into hosts or otherwise inaccessible places. The ovipositor is often modified into a stinger. The young develop through complete metamorphosis — that is, they have a worm-like larval stage and an inactive pupal stage before they mature.

Evolution

Hymenoptera originated in the Triassic, the oldest fossils belonging to the family Xyelidae. Social hymenopterans appeared during the Cretaceous. The evolution of this group has been intensively studied by A. Rasnitsyn, M. S. Engel, G. Dlussky, and others.

Anatomy

Hymenoptera are very small to large insects, usually with two pairs of wings. Their mouthparts are created for chewing, with well-developed mandibles. Many species have further developed the mouthparts into a lengthy proboscis, with which they can drink liquids, such as nectar. They have large compound eyes, and typically three ocelli.

The forward margin of the hind wing bears a number of hooked bristles, or "hamuli", which lock onto the fore wing, keeping them held together. The smaller species may have only two or three hamuli on each side, but the largest wasps may have a considerable number, keeping the wings gripped together especially tightly. Hymenopteran wings have relatively few veins compared with many other insects, especially in the smaller species.

In the more ancestral Hymenoptera, the ovipositor is blade-like, and has evolved for slicing plant tissues. In the majority, however, it is modified for piercing, and, in some cases, is several times the length of the body. In some species, the ovipositor has become modified as a sting, and the eggs are laid from the base of the structure, rather than from the tip, which is used only to inject venom. The sting is typically used to immobilise prey, but in some wasps and bees may be used in defence.

The larvae of the more ancestral Hymenoptera resemble caterpillars in appearance, and like them, typically feed on leaves. They have large chewing mandibles, three thoracic limbs, and, in most cases, a number of abdominal prolegs. Unlike caterpillars, however, the prolegs have no grasping spines, and the antennae are reduced to mere stubs.

The larvae of other Hymenoptera, however, more closely resemble maggots, and are adapted to life in a protected environment. This may be the body of a host organism, or a cell in a nest, where the adults will care for the larva. Such larvae have soft bodies with no limbs. They are also unable to defecate until they reach adulthood due to having an incomplete digestive tract, presumably to avoid contaminating their environment.

Sex determination

Among the hymenopterans, sex is determined by the number of chromosomes an individual possesses. Fertilized eggs get two sets of chromosomes (one from each parent's respective gametes), and so develop into diploid females, while unfertilized eggs only contain one set (from the mother), and so develop into haploid males; the act of fertilization is under the voluntary control of the egg-laying female. This phenomenon is called haplodiploidy.

Note, however, that the actual genetic mechanisms of haplodiploid sex determination may be more complex than simple chromosome number. In many Hymenoptera, sex is actually determined by a single gene locus with many alleles. In these species, haploids are male and diploids heterozygous at the sex locus are female, but occasionally a diploid will be homozygous at the sex locus and develop as a male instead. This is especially likely to occur in an individual whose parents were siblings or other close relatives. Diploid males are known to be produced by inbreeding in many ant, bee and wasp species.

One consequence of haplodiploidy is that females on average actually have more genes in common with their sisters than they do with their own daughters. Because of this, cooperation among kindred females may be unusually advantageous, and has been hypothesized to contribute to the multiple origins of eusociality within this order.

Diet

Different species of hymenoptera show a wide range of feeding habits. The most primitive forms are typically herbivorous, feeding on leaves or pine needles. Stinging wasps are predators, and will provision their larvae with immobilised prey, while bees feed on nectar and pollen.

A number of species are parasitoid as larvae. The adults inject the eggs into a paralysed host, which they begin to consume after hatching. Some species are even hyperparasitoid, with the host itself being another parasitoid insect. Habits intermediate between those of the herbivorous and parasitoid forms are shown in some hymenopterans, which inhabit the galls or nests of other insects, stealing their food, and eventually killing and eating the occupant.

Classification

Giant Honey Bee *Apis dorsata* on *Tribulus terrestris* in Hyderabad, India

Symphyta

The suborder Symphyta includes the sawflies, horntails, and parasitic wood wasps. The group may be paraphyletic, as it has been suggested that the family Orussidae may be the group from which the Apocrita arose. They have an unconstricted junction between the thorax and abdomen. The larvae are herbivorous free-living eruciforms, with three pairs of true legs, prolegs (on every segment, unlike Lepidoptera) and ocelli. The prolegs do not have crochet hooks at the ends unlike the larvae of the Lepidoptera.

Apocrita

The wasps, bees, and ants together make up the suborder Apocrita, characterized by a constriction between the first and second abdominal segments called a wasp-waist (petiole), also involving the fusion of the first abdominal segment to the thorax. Also, the larvae of all Apocrita do not have legs, prolegs, or ocelli.

Chapter 6

Orthoptera

Orthoptera Temporal range: Carboniferous–Recent 359–0 Ma	

Patanga japonica

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Orthopterida
(unranked):	Panorthoptera
Order:	**Orthoptera** Latreille, 1793

Extant suborders and superfamilies

Suborder Ensifera

- Grylloidea
- Hagloidea
- Rhaphidophoroidea
- Schizodactyloidea
- Stenopelmatoidea

- Tettigonioidea

Suborder Caelifera

- Acridoidea
- Eumastacoidea
- Pneumoroidea
- Pyrgomorphoidea
- Tanaoceroidea
- Tetrigoidea

- Tridactyloidea
- Trigonopterygoidea

Orthoptera is an order of insects with paurometabolous or incomplete metamorphosis, including the grasshoppers, crickets and locusts. Many insects in this order produce sound (known as a "stridulation") by rubbing their wings against each other or their legs, the wings or legs containing rows of corrugated bumps. The tympanum or ear is located in the front tibia in crickets, mole crickets, and katydids, and on the first abdominal segment in the grasshoppers and locusts. These organisms use vibrations to locate other individuals.

Grasshoppers are able to fold their wings, placing them in the group Neoptera.

Etymology

The name is derived from the Greek *ortho* meaning *straight* and *ptera* meaning *winged*.

Characteristics

Orthopterans have a generally cylindrical body, with hind legs elongated for jumping. They have mandibulate mouthparts and large compound eyes, and may or may not have ocelli, depending on the species. The antennae have multiple joints, and are of variable length.

The first and third segments of the thorax are enlarged, while the second segment is much shorter. They have two pairs of wings, which are held overlapping the abdomen at rest. The forewings, or tegmina, are narrower than the hindwings and hardened at the base, while the hind wing is membranous, with straight veins and numerous cross-veins. At rest, the hindwings are held folded fan-like under the forewings. The final two to three segments of the abdomen are reduced, and have single-segmented cerci.

Life cycle

Orthopteroid species have a paurometabolous life cycle or incomplete metamorphosis. The use of sound is generally crucial in courtship, and most species have distinct songs. Most grasshoppers lay their eggs in the ground or on vegetation. The eggs hatch and the young nymphs resemble adults but lack wings and at this stage are often called *hoppers*. They may often also have a radically different coloration from the adults. Through successive moults the nymphs develop wings until their final moult into a mature adult with fully developed wings.

The number of moults varies between species; growth is also very variable and may take a few weeks to some months depending on food availability and weather conditions.

Orthoptera as food

Orthopterans are the only insects considered kosher in Judaism. The list of dietary laws in the book of Leviticus forbids all flying insects that walk, but makes an exception for the locust. The Torah states the only kosher flying insects with four walking legs have knees that extend above their feet so that they hop. This suggests that non-jumping orthoptera such as mole crickets are not kosher.

Phylogenetics

The branching order of these animals is fairly well understood. The suborders *Caelifera* and *Ensifera* appear to be monophyletic and *Rhaphidophoridae* is a sister group of *Tettigoniidae*. *Pyrgomorphidae* are the most basal group of *Caelifera*. *Myrmecophilidae* appear to form a clade with *Gryllotalpidae* instead of with *Gryllidae*. Additional work may be needed to confirm this.

Among the four subfamilies of *Tettigoniidae* the relationships are - (*Phaneropterinae* + (*Conocephalinae* + (*Bradyporinae* + *Tettigoniinae*))) while among six acridid subfamilies were the relationships are -(*Oedipodinae* + (*Acridinae* + (*Gomphocerinae* + (*Oxyinae* + (*Calliptaminae* + *Cyrtacanthacridinae*))))).

Classification

- Suborder Ensifera
    - Superfamily Grylloidea
        - Gryllidae - true crickets
        - Gryllotalpidae - mole crickets
        - Mogoplistidae
        - Myrmecophilidae - ant crickets
    - Superfamily Hagloidea
        - Haglidae†

        - Hagloedischiidae†
        - Prophalangopsidae
        - Tuphellidae†
    - Superfamily Phasmomimoidea†
        - Phasmomimidae†
    - Superfamily Rhaphidophoroidea
        - Rhaphidophoridae — camel crickets, cave crickets, cave wetas
    - Superfamily Schizodactyloidea
        - Schizodactylidae — dune crickets
    - Superfamily Stenopelmatoidea
        - Anostostomatidae — wetas, king crickets
        - Cooloolidae
        - Gryllacrididae — leaf-rolling crickets
        - Stenopelmatidae — Jerusalem crickets
    - Superfamily Tettigonioidea
        - Haglotettigoniidae†
        - Tettigoniidae — katydids / bush crickets
- Suborder Caelifera — grasshoppers, locusts

Teratodus monticollis Hooded Grasshopper

- Infraorder Acrididea
  - Superfamily Acridoidea
    - Acrididae — grasshoppers, locusts
    - Charilaidae
    - Dericorythidae
    - Lathiceridae
    - Lentulidae
    - Lithidiidae
    - Ommexechidae
    - Pamphagidae — toad grasshoppers
    - Pyrgacrididae
    - Romaleidae
    - Tristiridae

        - Superfamily Eumastacoidea
            - Chorotypidae
            - Episactidae
            - Eumastacidae
            - Euschmidtiidae
            - Mastacideidae
            - Morabidae
            - Promastacidae†
            - Proscopiidae
            - Thericleidae

Proscopiid from the Andes of Peru

        - Superfamily Locustopsoidea†
            - Araripelocustidae†
            - Bouretidae†
            - Eolocustopsidae†
            - Locustavidae†
            - Locustopsidae†
        - Superfamily Pneumoroidea
            - Pneumoridae — bladder grasshoppers
        - Superfamily Pyrgomorphoidea
            - Pyrgomorphidae — gaudy grasshoppers
        - Superfamily Tanaoceroidea
            - Tanaoceridae
        - Superfamily Tetrigoidea
            - Tetrigidae — grouse locusts
        - Superfamily Trigonopterygoidea
            - Trigonopterygidae
            - Xyronotidae
    - Infraorder Tridactylidea
        - Superfamily Dzhajloutshelloidea†

    - Dzhajloutshellidae†
- Superfamily Regiatoidea†
    - Regiatidae†
- Superfamily Tridactyloidea
    - Cylindrachetidae
    - Ripipterygidae
    - Tridactylidae — pygmy mole crickets

Chapter 7

Plecoptera

Stoneflies Temporal range: 299–0 Ma Permian - Recent	

Adult of genus Eusthenia

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapoda
Class:	Insecta
Subclass:	Pterygota
Infraclass:	Neoptera
Superorder:	Exopterygota
Order:	**Plecoptera**

Burmeister, 1839

Suborders

Plecoptera are an order of insects, commonly known as **stoneflies**. There are some 3,497 described species worldwide, and new ones are still being discovered. Although stoneflies are found worldwide, they are absent from Antarctica. Stoneflies are believed to be one of the most primitive groups of Neoptera, with close relatives identified from the Carboniferous and Lower Permian geological periods, while true stoneflies are known from fossils only a bit younger. The modern diversity however apparently is of Mesozoic origin.

Plecoptera are found in both the Southern and Northern hemispheres, and the populations are quite distinct although the evolutionary evidence suggests that species may have crossed the equator on a number of occasions before once again becoming geographically isolated.

All species of Plecoptera are intolerant of water pollution and their presence in a stream or still water is usually an indicator of good or excellent water quality.

Description and ecology

Stonefly nymph

Stonefly adult

Stoneflies have a generalised anatomy, with few specialised features. They have simple mouthparts with chewing mandibles, long, multi-segmented antennae, large compound eyes and two or three ocelli. The legs are robust, with each ending in two claws. The abdomen is relatively soft, and may include remnants of the nymphal gills even in the adult. Both nymphs and adults have long paired cerci projecting from the tip of their abdomens.

The name "Plecoptera" literally means "braided-wings", from the Ancient Greek *plekein* (πλέκειν, "to braid") and *pteryx* (πτέρυξ, "wing"). This refers to the complex venation of their two pairs of wings, which are membranous and fold flat over the back. Stoneflies are generally not strong fliers, and some species are entirely wingless.

A few wingless species such as the Lake Tahoe Benthic Stonefly (*"Capnia" lacustra*) or *Baikaloperla* are the only known insects that are exclusively aquatic from birth to death. Some true water bugs (Nepomorpha) may also be fully aquatic for their entire life, but can leave the water to travel.

The females lay hundreds or even thousands of eggs in a ball which they initially carry about on their abdomen, and later deposit into the water. The eggs typically take two to three weeks to hatch, but some species undergo diapause, with the eggs remaining dormant throughout a dry season, and hatching only when conditions are suitable.

The nymphs are aquatic and live in the benthic zone of well-oxygenated lakes and streams. A few species found in New Zealand and nearby islands have terrestrial nymphs, but even these inhabit only very moist environments. The nymphs physically resemble wingless adults, but often have external gills, which may be present on almost any part of the body. In addition, they can also respire through the general body surface, and some even lack gills altogether. Most species are herbivorous as nymphs, feeding on submerged leaves and benthic algae, but many are hunters of other aquatic arthropods.

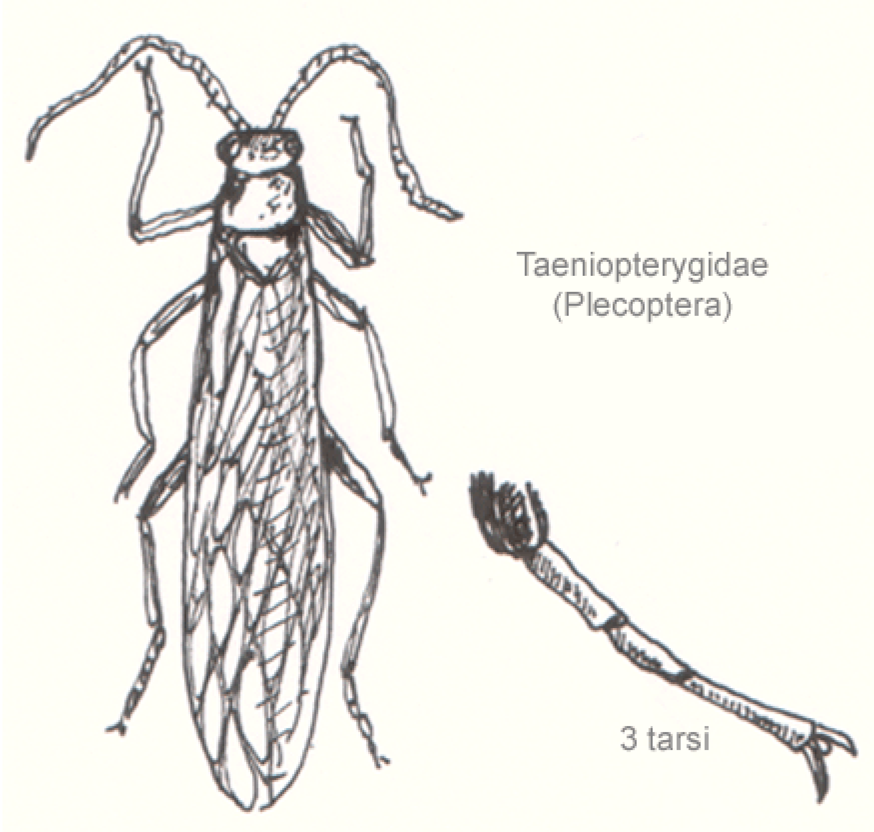
The insects remain in the nymphal form for one to four years, depending on species, and undergo anything from 12 to 33 molts before emerging and becoming terrestrial as adults. The adults generally only survive for a few weeks, and emerge only during specific times of the year. Some do not feed at all, but those that do are herbivorous.

Systematics

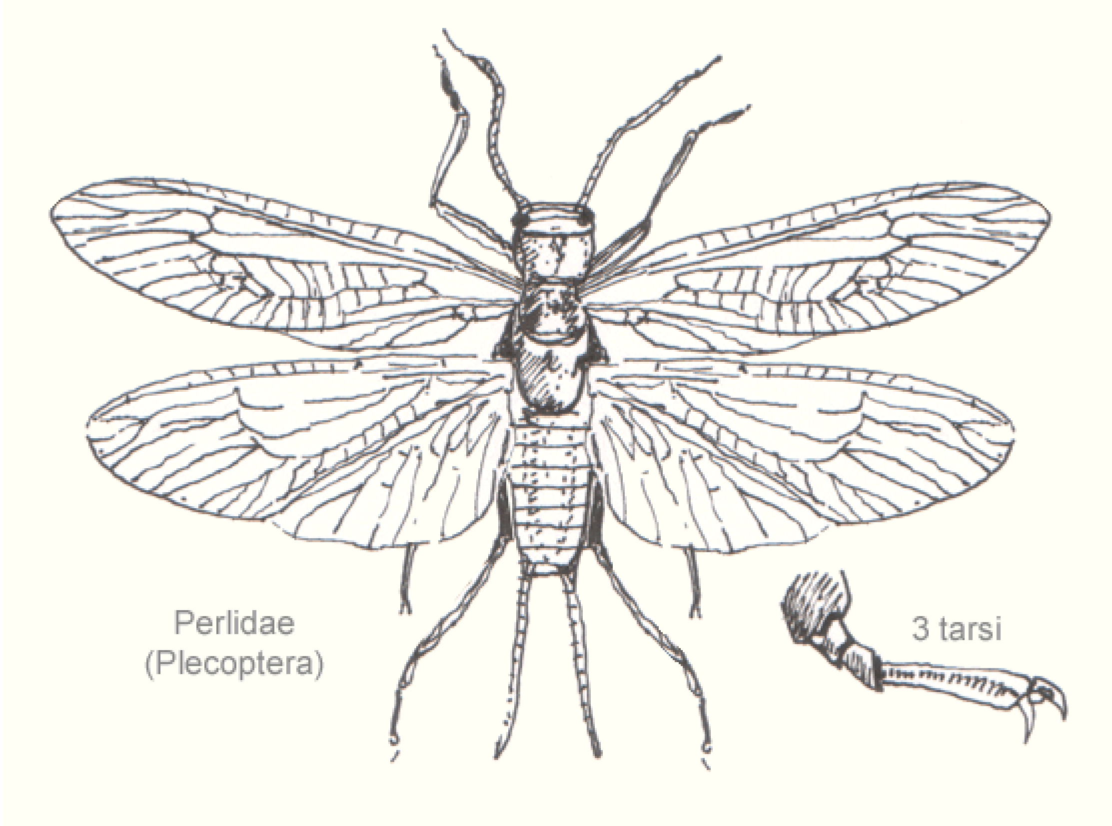
Traditionally, the stone flies were divided into two suborders, the **"Antarctoperlaria"** (or **"Archiperlaria"**) and the Arctoperlaria. However, the former simply consists of the two basalmost super families of stone flies, which do not seem to be each other's closest relatives. Thus, the "Antarctoperlaria" are not considered a natural group (despite some claims to the contrary).

The Arctoperlaria, meanwhile, have been divided into two infraorders, the Euholognatha (or Filipalpia) and the Systellognatha (also called Setipalpia or Subulipalpia). This corresponds to the phylogeny, with one exception: the Scopuridae must be considered a basal family in the Arctoperlaria, not assignable to any of the infra orders. Alternatively, the Scopuridae were placed in an unranked clade "Holognatha" together with the Euholognatha (meaning approximately "advanced Holognatha"). But the Scopuridae do not appear significantly closer to the Euholognatha than to the Systellognatha.

In addition, not adopting the clades Antarctoperlaria and Holognatha allows for a systematic layout of the Plecoptera that adequately reproduces phylogeny, while retaining the traditional ranked taxa.



Adult of family Taeniopterygidae (Euholognatha)



Adult of family Perlidae (Systellognatha)

Basal lineages ("Antarctoperlaria")

- Super family Eusthenioidea
    - Family Diamphipnoidae
    - Family Eustheniidae
- Super family Leptoperloidea
    - Family Austroperlidae
    - Family Gripopterygidae

Suborder Arctoperlaria

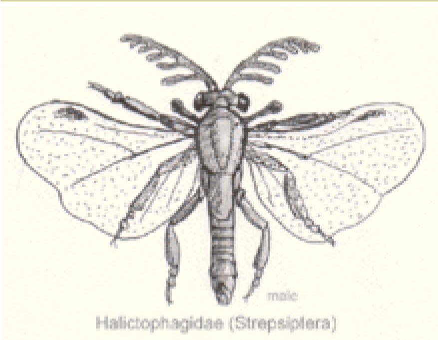
- Basal family Scopuridae
- Infraorder Euholognatha
    - Family Capniidae (ca. 300 species) - small winter stoneflies
    - Family Leuctridae (300+ species) - rolled-winged stoneflies
    - Family Nemouridae (600+ species) - spring stoneflies
    - Family Notonemouridae
    - Family Taeniopterygidae (ca. 75 species) - winter stoneflies
- Infraorder Systellognatha
    - Family Chloroperlidae (100+ species) - green stoneflies
    - Family Perlidae (ca. 400 species) - common stoneflies

- Family Perlodidae (250+ species)
- Family Peltoperlidae (ca. 68 species) - roachlike stoneflies
- Family Styloperlidae (ca. 10 species)
- Family Pteronarcyidae (ca. 12 species) - salmonflies, giant stoneflies

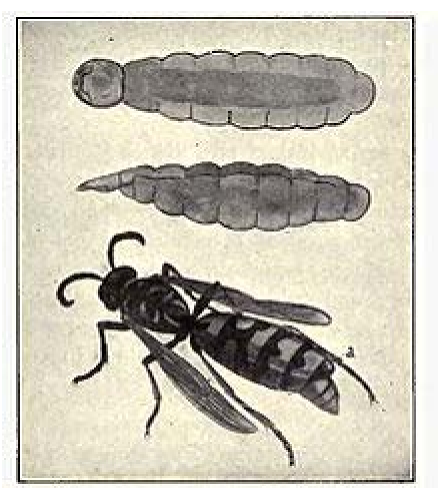
Chapter 8

Strepsiptera

Strepsiptera Temporal range: 125–0 Ma Middle Cretaceous - Recent



male



Female Strepsipteron, top and side views and a Stylopized Wasp: *a*, end of the parasite projecting between the abdominal segments of the Wasp. (*After Leuckart's Wandtafeln.*)

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta

Order:	**Strepsiptera** Kirby, 1813

Families
†Protoxenidae †Cretostylopidae †Mengeidae Bahiaxenidae Mengenillidae Stylopidae Bohartillidae Corioxenidae Halictophagidae Callipharixenidae Elenchidae Myrmecolacidae

The **Strepsiptera** (known in older literature as *twisted-winged parasites*) are an order of insects with ten families making up about 600 species. The early stage larvae and the short-lived adult males are free-living but most of their life is spent as endoparasites in other insects such as bees, wasps, leafhoppers, silverfish, and cockroaches.

Appearance and biology

Male Strepsiptera have wings, legs, eyes, and antennae, and look like flies, though they generally have no useful mouthparts. Many of their mouth parts are modified into sensory structures. Adult males are very short-lived (usually less than five hours) and do not feed. Females, in all families except the Mengenillidae, are not known to leave their hosts and are neotenic in form, lacking wings and legs. Virgin females release a pheromone which the males search for. In the Stylopidia the female has its anterior region extruding out of the host body and the male mates by rupturing the female's brood canal opening which lies between the head and prothorax. Sperm passes through the opening in a process termed hypodermic insemination. Each female produces many thousands of triungulin larvae that emerge from the brood opening on the head, which protrudes outside the host body. These larvae have legs (which lack a trochanter, the leg segment that forms the articulation between the basal coxa and the femur) and actively search out new hosts. Their hosts include members belonging to the orders Zygentoma, Orthoptera, Blattodea, Mantodea, Heteroptera, Hymenoptera, and Diptera. In the Strepsipteran family Myrmecolacidae, the males parasitize ants while the females parasitize Orthoptera.

Strepsiptera eggs hatch inside the female and the planidium larvae can move around freely within the female's haemocoel, which is unique to these animals. The female has a brood canal that communicates with the outside world and it is through this that the larvae escape. The larvae are very active, as they only have a limited amount of time to find a host before they exhaust their food reserves. These first-instar larvae have stemmata (simple, single-lens eyes) and once they latch onto a host they enter it by secreting enzymes that soften the cuticle, usually in the abdominal region of the host. Some species have been reported to enter the eggs of hosts. Larvae of *Stichotrema dallatorreanurn* Hofeneder from Papua New Guinea were found to enter their orthopteran host's tarsus (foot). Once inside the host, they undergo hypermetamorphosis and become a less mobile legless larval form. They induce the host to produce a bag-like structure inside which they feed and grow. This structure, made from host tissue, protects them from the immune defences of the host. Larvae go through four more instars and in each moult there is separation of the older cuticle but no discarding ("apolysis without ecdysis") leading to multiple layers being formed around the larvae. Male larvae produce pupae after the last moult, but females directly become neotenous adults. The colour and shape of the host's abdomen may be changed and the host usually becomes sterile. The parasites then undergo holometabolous metamorphosis to become adults. Adult males emerge out of the host body while females stay inside. Females may occupy up to 90% of the abdominal volume of their hosts.

Adult male Strepsiptera have eyes unlike those of any other insect, resembling the schizochroal eyes found in the trilobite group known as Phacopida. Instead of a compound eye consisting of hundreds to thousands of ommatidia, each with a single lens and capable of producing a picture element (pixel), the strepsipteran eyes consist of only a few dozen ommatidia separated by cuticle and/or setae, giving the eye a blackberry-like appearance.

Multiple females may be seen within a stylopized host. Males are rarely seen. They may sometimes be seen at light traps or may be lured using cages containing virgin females.

Strepsiptera may alter the behaviour of their hosts. Myrmecolacids may cause their ant hosts to climb up the tips of grass leaves, possibly to increase the spread of female pheromones to increase the chances of being located by males.

Classification

The order, named by William Kirby in 1813, is named for the hind wings (strepsi=twisted + ptera=wing), which are held at a twisted angle when at rest. The forewings are reduced to halteres (and initially thought to be dried and twisted).

Strepsiptera are an enigma to taxonomists. Originally it was believed they were the sister group to the beetle families Meloidae and Ripiphoridae, which have similar parasitic development and forewing reduction; early molecular research suggested their inclusion as a sister group to the flies, in a clade called the *halteria* which have one pair of the wings modified into halteres, and failed to support their relationship to the beetles. More recent molecular studies, however, suggest that they are outside the clade Mecopterida (containing the Diptera and Lepidoptera), yet there is no strong evidence for affinity with any other extant group. Study of their evolutionary position has been problematic due to difficulties in phylogenetic analysis arising from long branch attraction. The most basal strepsipteran is the fossil *Protoxenos janzeni* discovered in Baltic amber, while the most basal living strepsipteran is *Bahiaxenos relictus*, the sole member of the family

Bahiaxenidae. The earliest known strepsipteran fossil is that of *Cretostylops engeli* discovered in middle Cretaceous amber from Myanmar.

Families

The Strepsiptera have two major groups Stylopidia and Mengenillidia. The Mengenillidia include three extinct families (Cretostylopidae, Protoxenidae, and Mengeidae) plus two extant families (Bahiaxenidae and Mengenillidae; the latter is not monophyletic, however). They are considered more primitive and the known females (Mengenillidae only) are free living, with rudimentary legs and antennae. The females have a single genital opening. The males have strong mandibles, a distinct labrum, and more than 5 antennal segments.

The other group, Stylopidia, includes seven families Corioxenidae, Halictophagidae, Callipharixenidae, Bohartillidae, Elenchidae, Myrmecolacidae, and Stylopidae. All Stylopidia have endoparasitic females having multiple genital openings.

Stylopidae have 4 segmented tarsi and 4-6 segmented antennae with the third segment having a lateral process. The family Stylopidae may be paraphyletic. The Elenchidae have 2-segmented tarsi and 4 segmented antennae with the third segment having a lateral process. The Halictophagidae have 3-segmented tarsi and 7-segmented antennae with lateral processes from the third and fourth segments. The Stylopidae mostly parasitize wasps and bees, the Elenchidae are known to parasitize Fulgoroidea while the Halictophagidae are found on leafhoppers, treehoppers as well as mole cricket hosts.

Chapter 9

Caddisfly

Caddisflies Temporal range: Triassic–Recent	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Amphiesmenoptera
Order:	**Trichoptera** Kirby, 1813
Suborders	

- Annulipalpia
- Spicipalpia
- Integripalpia

The **caddisflies** are an order, **Trichoptera**, of insects with approximately 12,000 described species. Also called **sedge-flies** or **rail-flies**, they are small moth-like insects having two pairs of hairy membranous wings. They are closely related to Lepidoptera (moths and butterflies) which have scales on their wings, and the two orders together form the superorder Amphiesmenoptera. Caddisflies have aquatic larvae and are found in a wide variety of habitats such as streams, rivers, lakes, ponds, spring seeps, and temporary waters (vernal pools). The larvae of many species make protective cases of silk decorated with gravel, sand, twigs or other debris. The name "Trichoptera" comes from Greek: θρίξ (*thrix*, "hair") + πτερόν (*pteron*, "wing").

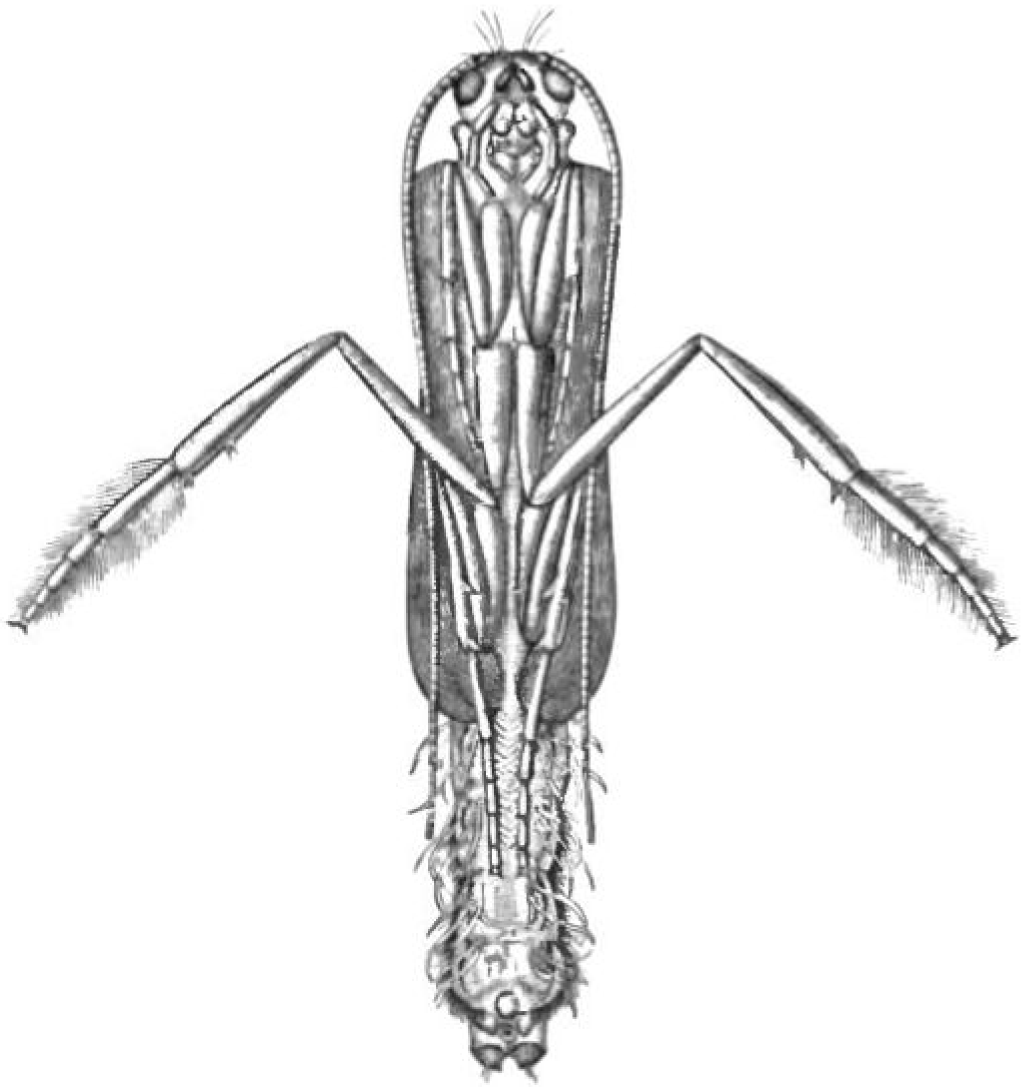
Ecology

Although caddisflies may be found in waterbodies of varying qualities, species-rich caddisfly assemblages are generally thought to indicate clean water. Together with stoneflies and mayflies, caddisflies feature importantly in bioassessment surveys of streams and other water bodies. Caddisfly species can be found in all feeding guilds in stream habitats, with some species being predators, leaf shredders, algal grazers, and collectors of particles from the watercolumn and benthos.

Underwater architects

Caddisfly larva with portable case of rock fragments

Caddisfly larva emerging from case made of plant material



Pupa of Caddis-fly in swimming position.
Twice natural size.

Pupa of caddisfly

Close-up of spun case of caddisfly larva. BC, Canada

A "net" made by caddisfly larva. Texas, United States

Caddisflies are considered underwater architects because many species use silk for building throughout their larval life. Caddisflies can be loosely divided into three behavioral groups based on this use of silk: retreat-making caddisflies, case-making caddisflies, and free-living caddisflies. Those that build retreats build a net or retreat from silk and other materials and use it to catch food items such as algae, aquatic invertebrates and zooplankton from the flowing stream. Case-making caddisflies make portable cases using silk along with substrate materials such as small fragments of rock, sand, small pieces of twig, aquatic plants, or sometimes silk alone. Many use the retreats or cases throughout their larval life, adding to, or enlarging them as they grow. These may look very much like bagworm cases, which are constructed by various moth species that are not aquatic. Free-living caddisflies do not build retreats or carry portable cases until they are ready to pupate.

Development

Many species of caddisfly larvae enter a stage of inactivity called the pupa stage for weeks or months after they mature but prior to emergence. Their emergence is then triggered by cooling water temperatures in the fall, effectively synchronizing the adult activity to make mate-finding easier. In the Northwestern US, caddisfly larvae within their gravel cases are called 'periwinkles.'

Caddisfly pupation occurs much like pupation of Lepidoptera. That is, caddisflies pupate in a cocoon spun from silk. Caddisflies which build the portable cases attach their case to some underwater object, seal the front and back apertures against predation though still allowing water flow, and pupate within it. Once fully developed, most pupal caddisflies cut through their cases with a special pair of mandibles, swim up to the water surface, cast off skin and the now-obsolete gills and mandibles, and emerge as fully formed adults. In a minority of species, the pupae swim to shore and crawl out to emerge. Many of them are able to fly immediately after breaking from their pupal skin.

The adult stage of caddisflies, in most cases, is very short-lived, usually only 1–2 weeks, but can sometimes last for 2 months. Most adults are non-feeding and are equipped mainly to mate. Once mated, the female caddisfly will often lay eggs (enclosed in a gelatinous mass) by attaching them above or below the water surface. Eggs hatch in as little as three weeks.

Caddisflies in most temperate areas complete their life cycles in a single year. The general temperate-zone lifecycle pattern is one of larval feeding and growth in autumn, winter, and spring, with adult emergence between late spring and early fall, although the adult activity of a few species peaks in the winter. Larvae are active in very cold water and can frequently be observed feeding under ice. In common with many aquatic insect species, many caddisfly adults emerge synchronously *en masse*. Such emergence patterns ensure that most caddisflies will encounter a member of the opposite sex in a timely fashion. Mass emergences of this nature are called 'hatches' by salmon and trout anglers, and salmonid fish species will frequently 'switch' to whatever species is emerging on a particular day. Anglers take advantage of this behavior by matching their artificial flies to the appropriate fly.

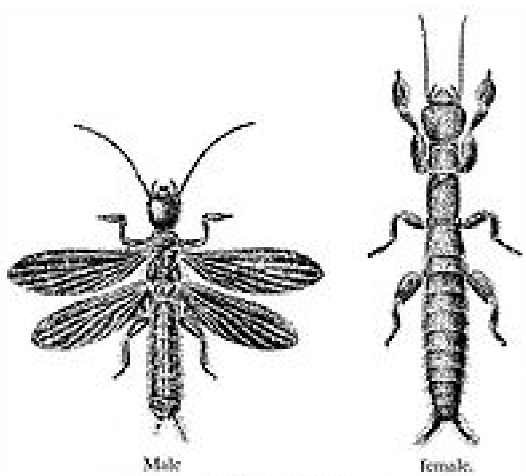
Classification

Two or three suborders are recognised. Annulipalpia and Integripalpia are universally recognised, while the monophyly of Spicipalpia is disputed.

Chapter 10

Embioptera

Embioptera **Temporal range: 199–0 Ma** **Jurassic – Recent**	



Embia major (Embioptera).
From A. D. Imms, 1913, On *Embia major* n. sp. From the Himalayas, *Trans. Linn. Soc. Zool.* 11:167–195.

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Subclass:	Pterygota
Infraclass:	Neoptera
Order:	**Embioptera** Lameere, 1900

Families

There are 2 suborders and 10 families:

- Andesembiidae

- Anisembiidae
- Australembiidae
- Clothodidae
- Embiidae
- Embonychidae
- Notoligotomidae
- Oligotomidae
- Teratembiidae
- Sorellembiidae

The order **Embioptera**, commonly known as **webspinners**, are a small group of mostly tropical and subtropical insects, classified under the subclass Pterygota. The order has also been referred to as **Embiodea** or **Embiidina**. The name Embioptera ("lively wings") comes from Greek, *embios* meaning "lively" and *pteron* meaning "wing", a name that has not been considered to be particularly descriptive for this group of fliers. Perhaps instead referring to their remarkable speed of movement both forward and backward. The group probably first appeared during the Jurassic and is well represented in Cretaceous amber. The common name *webspinner* comes from the insects' ability to spin silk from structures on their front legs. They use the silk to make a web-like pouch or gallery in which they live.

Over 360 embiopteran species have been described, along with estimates of around 2000 species being in existence today. There is some debate as the exact phylogenetic classification of Embioptera, having been classed as a sister group to both orders Zoraptera, and Phasmatodea, and there is continuing dispute today as to the accuracy of these classifications.

The order is distributed all over the world, being found on every continent except Antarctica, with the highest density and diversity of species being located in tropical regions.

Description

All webspinners have a remarkably similar body form, although they do vary in colouration and size. The majority of embiids are brown or black in colour, ranging through to a pink or reddish shades in some species, and range in size from 1.5 to 2.0 millimetres (0.059 to 0.079 in). The body form of these insects is completely specialised for the silk tunnels and chambers in which they reside, being long, narrow and highly flexible. All the females and larvae are wingless, whereas males can be either winged or wingless depending on species. . The head has projecting mouthparts with chewing mandibles. The compound eyes are kidney-shaped, there are no ocelli, and the antennae are long, with up to 32 segments.

The body is cylindrical in form, adapted for the tubular galleries within which the insects live. The first segment of the thorax is small and narrow, while the second and third are larger and broader, especially in the males, where they include the flight muscles. The wings, where present, occur as 2 pairs that are similar in size and shape: long and narrow, with relatively simple venation. These wings operate using basic hydraulics; pre-flight, chambers within the wings fill with hemolymph, making them rigid enough for use. On landing these chambers empty and wings become flexible, folding back against the body. Wings can also fold forwards over the body, and this, along with the flexibility allows easy movement through the narrow silk galleries without resulting in damage.

Adult winged male *Oligotoma saundersii*

In both males and females the legs are short and sturdy, with an enlarged tarsomere on the first pair, containing the silk-producing glands. The abdomen has ten segments, with a pair of cerci on the final segment. These cerci are highly sensitive to touch, and allow the animal to navigate while moving backwards through the gallery tunnels, which are too narrow to allow the insect to turn round. Because morphology is so similar between embiid species, it makes species identification extremely difficult. For this reason, the main form of taxonomic identification used in the past has been close observation of distinctive copulatory structures of males, (although this method is now thought by some entomologists and taxonomists as giving insufficient classification detail). Although males never eat during their life span, they do have mouthparts similar to the females. These mouthparts are used to hold onto the female during copulation.

Life cycle

Embiopteran egg on gallery wall

Embiopteran nymph

After mating, the female lays a single batch of eggs either within the existing gallery, or will find new territory to start a new colony. Here, the eggs hatch into nymphs that resemble small, wingless adults (images right and below). After a short period of parental care, the nymphs undergo hemimetobolosis (moulting into several immature stages before emerging as a fully grown adult after the last moult), moulting a total of four times before reaching adult form. Adult males never eat, and leave the home colony almost immediately to find a female and mate. Those males who can not fly will often mate with females in nearby colonies, meaning their chosen mates are often siblings or closely related. In some species, the female will eat the male after mating, but in any event, the male will not survive for long after mating. A few species are known to be parthenogenetic, meaning they are able to produce viable offspring without fertilisation of eggs. This phemonenon occurs when a female is, for whatever reason, unable to find a male to mate with, thus giving her and her species reproductive security at all times.

Diet

The embiopteran diet varies between species, with available food sources changing with varying habitat. The nymphs and adult females are herbivorous, feeding on leaf litter, moss, bark and lichen. As stated above, adult males do not eat at all, meaning the majority die rapidly due to depleted energy resources (starvation).

Social behaviour

A 1st instar larval embiid in gallery

Most, if not all embiopteran species, like many other species of insect, are gregarious, specifically displaying subsociality. This particular kind of social behaviour involves the female embiid guarding her eggs and then caring for her young (right) for several days after hatching. In some species this parental care even involves the female feeding the nymphs with portions of chewed-up leaf litter and other food sources.

Subsociality is a trade-off for the female embiid, as the energy and time that is exerted into caring for her young is rewarded by giving them a much greater chance of surviving and carrying on her genetic lineage. Some species do share galleries with more than one adult, however most groups consist of one adult female and her offspring.

Silk web production

Embiopterans produce a silk thread highly similar to that produced by the much better known silkworm *Bombyx mori*. The silk is produced in spherical secretary glands in the tarsi of the embiids enlarged forelimbs, and can be produced by both adults and larvae. Unlike *Bombyx mori* and other silk-producing (and spinning) members of both Lepidoptera and Hymenoptera, which only have one pair of silk glands per individual, some species of embiid are estimated to have up to 300 silk glands: 150 in each forelimb. These glands are linked to 'setae-like cuticular process called a silk ejector', and their exceedingly high numbers allow individuals to spin large amounts of silk very quickly, creating extensive galleries (see image below). The silk web is produced throughout all stages of the embiopteran lifespan, and requires very little energy output.

Galleries

Adult female embiid in gallery

The ‘galleries' produced by embiids are tunnels and chambers woven from the silk they produce. These woven constructions can be found on substrates such as rocks and the bark of trees, or in leaf litter. Some species camouflage their galleries by deccorating the outer layers with bits of leaf litter or other materials to match their surroundings. The galleries are essential to their life cycle, maintaining moisture in their environment, plus offering protection from predators and elements while foraging, breeding and simply existing. The only occasion when an embiid will leave the gallery complex is when winged males fly out or wingless males walk out in search of a mate, or when females explore the area immediately surrounding them in search of a new food source. On detection of a potential predator or threat, the embiids retreat into their galleries, and some species have even been observed to 'play dead' until the threat is no longer present.

Webspinners continually extend their galleries into new food sources, and expand their existing galleries as they grow in size. The insects spin silk by moving their forelegs back and forth over the substrate, and rotating their bodies to create a cylindrical, silk-lined tunnel. Older galleries have multiple laminate layers of silk. Each gallery complex contains a number of individuals, often descended from a single female, and forms a complex maze-like structure, extending from a secure retreat into whatever vegetable food matter is available nearby. The size and complexity of the colony varies between species, and they can be very extensive in those species that live in hot and humid climates.

Chapter 11

Mecoptera

Mecoptera **Temporal range: Permian - Recent** **299–0 Ma**	
	
Panorpa communis, male	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Panorpida
(unranked):	Antliophora
Order:	**Mecoptera** Hyatt & Arms, 1891
Families	

- Apteropanorpidae
- Bittacidae (hangingflies)
- Boreidae (snow scorpionflies)
- Choristidae
- †Dinopanorpidae
- Eomeropidae
- Meropeidae (earwigflies)
- Nannochoristidae

- Panorpidae (common scorpionflies)
- Panorpodidae (short-faced scorpionflies)

Mecoptera are an order of insects with about 550 species in nine families worldwide. Mecoptera are sometimes called **scorpionflies** after their largest family, Panorpidae, in which the males have enlarged genitals that look similar to the stinger of a scorpion. The Bittacidae, or **hangingflies**, are a prominent family of elongate insects known for their elaborate mating rituals, in which females choose mates based on the quality of gift prey offered by various males.

While modern mecoptera are overwhelmingly predators or consumers of dead organisms, early ones might have played an important role before the evolution of other insects in pollinating extinct gymnosperms.

Anatomy and biology

Mecoptera are small to medium insects with slender, elongated, bodies. They have relatively simple mouthparts, with long mandibles and fleshy palps, which resemble those of the more primitive true flies. Like many other insects, they possess compound eyes on the side of the head, and three ocelli on the top. Most Mecoptera feed on vegetation in moist environments; in hotter climates, they may therefore be active only for short periods of the year.

The wings are narrow in shape, with numerous cross-veins, and somewhat resemble those of primitive insects such as mayflies. A few genera, however, have reduced wings, or have lost them altogether. The abdomen is cylindrical, and typically curves upwards in the male, superficially resembling the tail of a scorpion.

The female lays the eggs in close contact with moisture, and the eggs typically absorb water and increase in size after deposition. In species that live in hot conditions, the eggs may not hatch for several months, the larvae only emerging when the dry season has finished. More typically, however, they hatch after a relatively short period of time.

The larvae are usually quite caterpillar-like, with short, clawed, true legs, and a number of abdominal prolegs. They have a sclerotised head with compound eyes and mandibulate mouthparts. The tenth abdominal segment bears either a suction disc, or, less commonly, a pair of hooks. They generally eat vegetation or scavenge for dead insects, although some predatory larvae are known.

The larva crawls into the soil or decaying wood to pupate, and does not spin a cocoon. The pupae are exarate, meaning that the limbs are free of the body, and are able to move their mandibles, but are otherwise entirely non-motile. In drier environments, they may spend several months in diapause, before emerging as adults once the conditions are more suitable.

Evolution

DNA evidence indicates that fleas, which are traditionally considered a separate order (Order Siphonaptera), are instead highly specialized Mecoptera. Grouped together with the fleas, Mecoptera would have about 3000 known species.

Mecoptera have special importance in evolution of Insecta. Two of the most important insect orders, Lepidoptera and Diptera, along with Trichoptera, probably evolved from ancestors belonging to, or strictly related to, the Mecoptera. This is apparent from anatomical and biochemical similarities, but, moreover, transitional fossils, such as *Permotanyderus* and *Choristotanyderus*, have been discovered that lie between the Mecoptera and Diptera.

The group was once much more widespread and diverse than at present, having as many as four suborders during the Mesozoic.

First pollinators

It has been proposed that extinct mecoptera species were important plant pollinators. Early non-angiosperm gymnosperm seed plants during the late Middle Jurassic to mid–Early Cretaceous period have been believed to be mainly wind-pollinated. However examination of fossil mecoptera show that they had siphon feeding apparatus that could fertize early gymnosperms by feeding on their nectar and pollen. The lack of iron enrichment in their fossilized proboscis rules out a use in blood drinking. One question over this suggestion is that so far pollen has not been found associated with these feeding parts which is surprising for the amber-encased insects which should have preserved pollen but "further fossils may provide this information".

11 species have been identified belonged to three families, Mesopsychidae, Aneuretopsychidae, and Pseudopolycentropodidae for which "the encompassing name Aneuretopsychina is available". There length ranges from 3 mm in Parapolycentropus burmiticus to 28 mm in Lichnomesopsyche gloriae. The proboscis could be as long as 10 mm. Pollen transfer has been suggested to occur by body surface transport on mouthpart and head surfaces like that in bee flies and hover flies—however no such associated pollen has been found even though the insects were preserved in amber. It is thought that they pollinated such plants as Caytoniaceae, Cheirolepidiaceae, Czekanowskiaceae, Pentoxylaceae, and Gnetales as these have ovulate organs that are either poorly suited for wind pollination or have structures that could support long-proboscid fluid feeding.

Male genital (*Panorpa communis*)

Panorpa meridionalis, from Portugal

Bittacidae species from Australia

Panorpa communis female with prey

Panorpa communis male

Detail of head, male (*Panorpa communis*)

Dinokanaga andersoni Forewing

Male *Panorpa communis*

Chapter 12

Megaloptera and Neuroptera

Megaloptera

Megaloptera Temporal range: Permian–Recent	
	
Alderfly of the genus *Sialis*	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Infraclass:	Neoptera
(unranked):	Eumetabola
(unranked):	Endopterygota
Order:	**Megaloptera**
Families	

Megaloptera is an order of insects. It contains the alderflies, dobsonflies and fishflies, and there are about 300 known species.

The Megaloptera were formerly considered part of a group then called Neuroptera, together with lacewings and snakeflies, but these are now generally considered to be separate orders, with Neuroptera referring to the lacewings and relatives (which were formerly called Planipennia). The former Neuroptera - particularly the lacewing group - are nonetheless very closely related to each other, and the new name for this group is Neuropterida. This is either placed at superorder rank, with the Endopterygota - of which they are part - becoming an unranked clade above it, or the Endopterygota are maintained as a superorder, with an unranked Neuropterida being a part of them. Within the endopterygotes, the closest living relatives of the neuropteridan clade are the beetles.

The order's name comes from Ancient Greek - from *mega-* (μέγα-) "large" + *pteryx* (πτέρυξ) "wing" -, in reference to the large, clumsy wings of these insects. Megaloptera are relatively unknown insects across much of their range, due to the adults' short lives, the aquatic larvae's tolerance to pollution which is often rather high (so they are not often encountered by swimmers etc.), and the generally crepuscular or nocturnal habits. However, in the Americas the dobsonflies are rather well-known, as their males have tusk-like mandibles. These, while formidable in appearance, are relatively harmless to humans, as well as all other organisms; much like a peacock's feathers they serve no purpose other than to impress females, and in addition to hold them during mating. Hellgrammites, which are dobsonfly larvae, are often used for angling bait in North America.

Anatomy and life cycle

Adult Megalopterans closely resemble the lacewings, except for the presence of a pleated region on their hind wings, helping them to fold over the abdomen. They have strong mandibles and mouthparts apparently adapted for chewing, although many species do not eat as adults. They have large compound eyes, and, in some species, also have ocelli. The wings are large and subequal.

The female lays thousands of eggs in a single mass, placing them on vegetation overhanging water. Megaloptera undergo the most rudimentary form of complete metamorphosis among the insects. There are fewer differences between the larval and adult forms of Megaloptera than in any other order of holometabolous insects, and their aquatic larvae dwell in fresh water, around which the adults also live. The larvae are carnivorous, possessing strong jaws that they use to capture other aquatic insects. They have large heads and elongated bodies. The abdomen bears a number of fine tactile filaments, which, in some species, may include gills. The final segment of the abdomen bears either a pair of prolegs, or a single, tail-like appendage.

The larvae grow slowly, taking several years to reach the last larval stage. When they reach maturity, the larvae crawl out onto land to pupate in damp soil or under logs. Unusually, the pupa is fully motile, with large mandibles that it can use to defend itself against predators. The short-lived adults emerge from the pupa to mate - many species never feed as adults, living only a few days or hours.

Evolution

Apart from the two living families, there are a few prehistoric taxa in the Megaloptera, only known from fossils. Some of these occupy a more basal position:

- Genus *Corydasialis* (sometimes considered monotypic family Corydasialidae)
- Family Parasialidae (probably paraphyletic)
- Family Euchauliodidae

Neuroptera

Neuroptera
Temporal range: 299–0 Ma
Permian to Recent

Green lacewing

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Subclass:	Pterygota
Infraclass:	Neoptera
Superorder:	Endopterygota or Neuropterida
Order:	**Neuroptera** Linnaeus, 1758

Suborders

- Hemerobiiformia

- Myrmeleontiformia

The insect order **Neuroptera**, or **net-winged insects**, includes the lacewings, mantidflies, antlions, and their relatives. The order contains some 6,010 species. Traditionally, the group that was once known as **Planipennia**, with the Neuroptera at that time also including alderflies, fishflies, dobsonflies and snakeflies, but these are now generally considered to be separate orders (the Megaloptera and Raphidioptera). Sometimes the name Neuropterida is used to refer to these three orders as a group. This is either placed at superorder rank, with the Endopterygota becoming an unranked clade above it, or the Endopterygota are maintained as a superorder, with an unranked Neuropterida being a part of them. Within the endopterygotes, the closest living relatives of the neuropteridan clade are the beetles. The common name **lacewings** is often used for the most widely known net-winged insects - the green lacewings (Chrysopidae) - but actually most members of the Neuroptera are referred to as some sort of "lacewing".

The adults of this order possess four membranous wings, with the forewings and hindwings about the same size, and with many veins. They have chewing mouthparts, and undergo complete metamorphosis.

Neuropterans first appeared during the Permian Period, and continued to diversify through the Mesozoic Era. During this time several unusually large forms evolved, especially in the extinct family Kalligrammatidae, often referred to as "the butterflies of the Jurassic" due to their large, patterned wings.

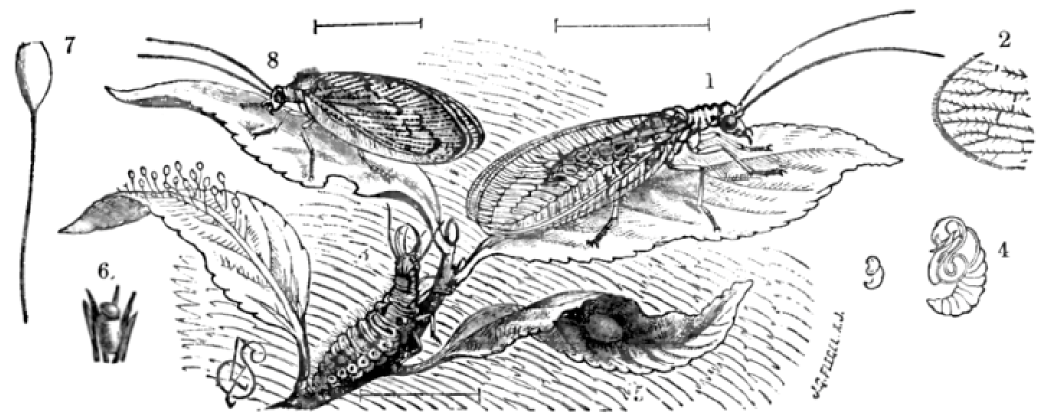
Anatomy and biology

Neuropterans are soft-bodied insects with relatively few specialised features. They have large lateral compound eyes, and may or may not also have ocelli. Their mouthparts have strong mandibles suitable for chewing, and lack the various adaptations found in most other endopterygote insect groups.

They have four wings, which are usually similar in size and shape, have a generalised pattern of veins. Some Neuropterans have specialised sense organs in their wings, or have bristles or other structures to link their wings together during flight.

The larvae are specialised predators, with elongated mandibles adapted for piercing and sucking. The larval body form varies between different families, depending on the nature of their prey. In general, however, they have three pairs of thoracic legs, each ending in two claws. The abdomen often has adhesive discs on the last two segments.

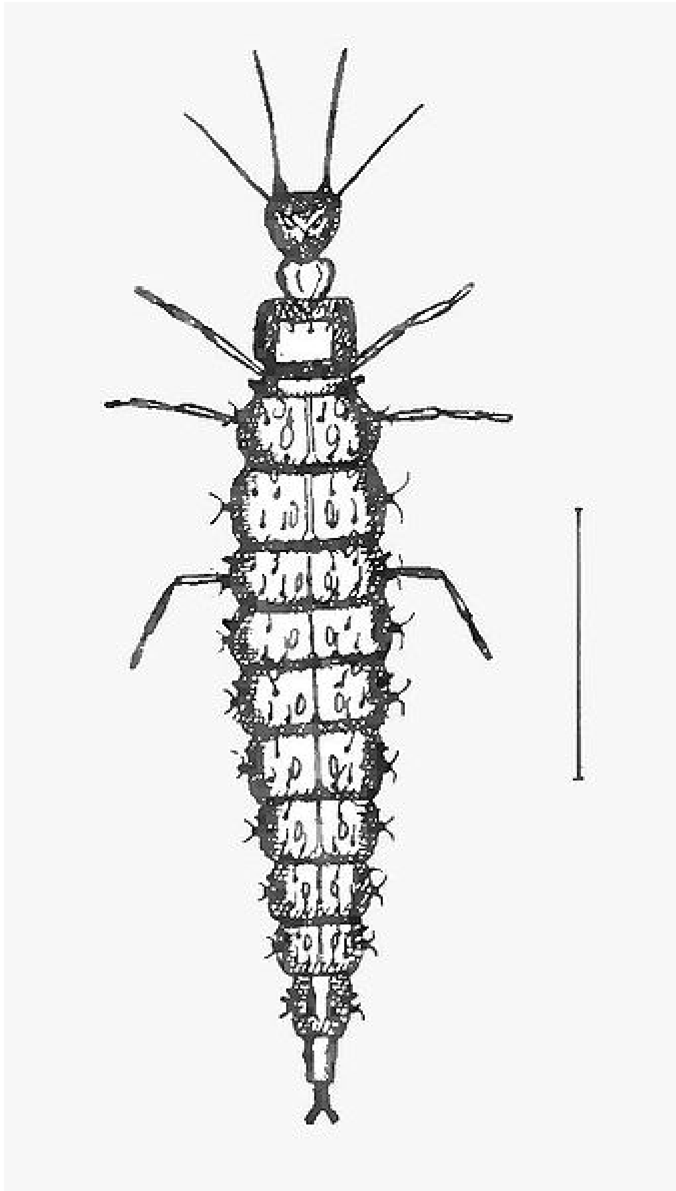
Life cycle and ecology



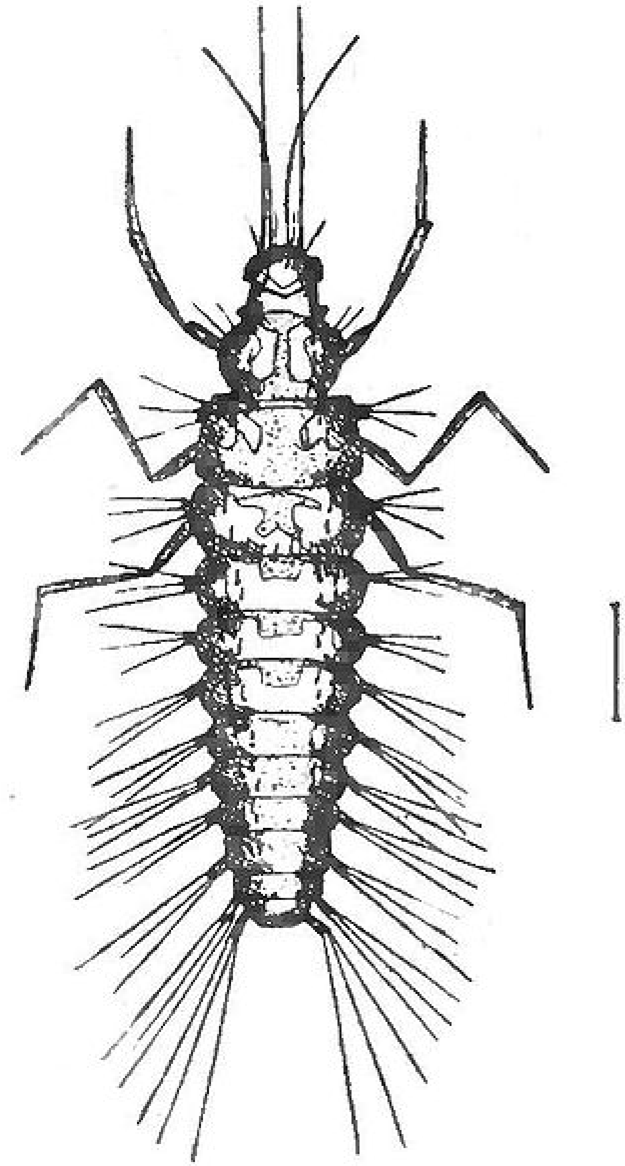
LACE-WING FLIES.

1, *Chrysopa vulgaris*; 2, The tip of its wing; 3, Larva; 4, Pupa; 5, 6, Cocoon; 7, Egg; 8, *Hemerobius hirtus*.

Life cycle of lacewings



Larva of *Osmylus fulvicephalus*, Osmylidae



Larva of *Sisyra* sp., Sisyridae

The larvae of most families are predators. Many chrysopids eat aphids and other pest insects, and have been used for biological control (either from commercial distributors but also abundant and widespread in nature). Larvae in various families cover themselves in debris (sometimes including dead prey insects) as camouflage, taken to an extreme in the ant lions, which bury themselves completely out of sight and ambush prey from "pits" in the soil. Larvae of some Ithonidae are root feeders, and larvae of Sisyridae are aquatic, and feed on freshwater sponges. A few mantispids are parasites of spider egg sacs.

As in other holometabolic orders, there is a pupal stage, generally enclosed in some form of cocoon composed of silk and soil or other debris. The pupa eventually cuts its way out of the cocoon with its mandibles, and may even move about for a short while before undergoing the moult to the adult form.

Adults of many groups are also predatory, but some do not feed, or consume only nectar.

Taxonomy and systematics

The understanding of neuropteran phylogeny has vastly improved since the mid-1990s, not the least courtesy of the ever-growing fossil record. In 1995, for example, it was simply known that the Megaloptera and Raphidioptera were not part of the Neuroptera in the strict sense, and the Mantispoidea and part of the Myrmeleontoidea were the only groups that could be confirmed by cladistic analysis. Though the relationships of some families remain to be fully understood, most major lineages of Neuropterida can nowadays be robustly placed in an evolutionary context.

A 49-million-year-old fossil wing of *Palaeopsychops marringerae* (Polystoechotidae), showing color pattern

Chrysoperla carnea (Chrysopidae)

Drepanepteryx phalaenoides (Hemerobiidae)

Ditaxis biseriata (Mantispidae)

Kalligramma haeckeli fossil (Kalligrammatidae)

Apart from a few groups that are quite basal or of uncertain position, the net-winged insects can be divided into two suborders, the Myrmeleontiformia and the Hemerobiiformia. The primitive Nevrorthidae, the most ancient group of living neuropterans, are sometimes considered a third suborder Nevrorthiformia or included in the Hemerobiiformia and more specifically in the Osmyloidea. But actually they are better considered a very basal lineage.

Basal and unresolved forms

- Genus *Mantispidiptera* Grimaldi, 2000 (Late Cretaceous; New Jersey; formerly Mantispidae)
- Genus *Mesohemerobius* Ping, 1928(Late Jurassic/Early Cretaceous; China)
- Family Permithonidae (fossil, probably paraphyletic)
- Family Prohemerobiidae (fossil, probably paraphyletic)
- Family Nevrorthidae
- Family Grammosmylidae (fossil)

Suborder Hemerobiiformia

- *Incertae sedis*
    - Family Osmylitidae (fossil, probably paraphyletic)
- Superfamily Ithonioidea
    - Family Ithonidae: moth lacewings (includes Rapismatidae)
    - Family Polystoechotidae: giant lacewings (formerly in Hemerobioidea)
- Superfamily Osmyloidea
    - Family Osmylidae: osmylids
- Superfamily Chrysopoidea
    - Family Ascalochrysidae (fossil)
    - Family Mesochrysopidae (fossil)
    - Family Chrysopidae: green lacewings, stinkflies (formerly in Hemerobioidea)
- Superfamily Hemerobioidea
    - Family Hemerobiidae: brown lacewings
- Superfamily Coniopterygoidea
    - Family Coniopterygidae: dustywings
    - Family Sisyridae: spongillaflies (formerly in Osmyloidea, tentatively placed here)
- Superfamily Mantispoidea
    - Family Dilaridae: pleasing lacewings (formerly in Hemerobioidea)
    - Family Mantispidae: mantidflies
    - Family Mesithonidae (fossil, probably paraphyletic)
    - Family Rhachiberothidae: thorny lacewings
    - Family Berothidae: beaded lacewings

Suborder Myrmeleontiformia

- Superfamily Nemopteroidea
    - Family Kalligrammatidae (fossil)
    - Family Psychopsidae: silky lacewings (formerly in Hemerobioidea)
    - Family Nemopteridae: spoonwings, spoon-winged laceflies, thread-winged laceflies (formerly in Myrmeleontoidea)
- Superfamily Myrmeleontoidea
    - Family Osmylopsychopidae (fossil)
    - Family Nymphitidae (fossil)
    - Family Solenoptilidae (fossil, probably paraphyletic)
    - Family Brogniartiellidae (fossil)
    - Family Nymphidae: split-footed lacewings (includes Myiodactylidae)
    - Family Babinskaiidae (fossil)
    - Family Myrmeleontidae: antlions (includes Palaeoleontidae)
    - Family Ascalaphidae: owlflies, ascalaphids

Chapter 13

Louse

Phthiraptera	

Light micrograph of *Fahrenholzia pinnata*

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Subclass:	Pterygota

Infraclass:	Neoptera
Order:	**Phthiraptera** Haeckel, 1896
Suborders	

Anoplura
Rhyncophthirina
Ischnocera
Amblycera

Lice (singular: **louse**) is the common name for over 3000 species of wingless insects of the order Phthiraptera; three of which are classified as human disease agents. They are obligate ectoparasites of every avian and mammalian order except for Monotremes (the platypus and echidnas), bats, whales, dolphins, porpoises and pangolins.

Biology

Most lice are scavengers, feeding on skin and other debris found on the host's body, but some species feed on sebaceous secretions and blood. Most are found only on specific types of animal, and, in some cases, only to a particular part of the body; some animals are known to host up to fifteen different species, although one to three is typical for mammals, and two to six for birds. For example, in humans, different species of louse inhabit the scalp and pubic hair. Lice generally cannot survive for long if removed from their host.

A louse's color varies from pale beige to dark gray; however, if feeding on blood, it may become considerably darker. Female lice are usually more common than the males, and some species are even known to be parthenogenetic. A louse's egg is commonly called a nit. Many lice attach their eggs to their host's hair with specialized saliva; the saliva/hair bond is very difficult to sever without specialized products. Lice inhabiting birds, however, may simply leave their eggs in parts of the body inaccessible to preening, such as the interior of feather shafts. Living lice eggs tend to be pale white. Dead lice eggs are more yellow.

Lice are exopterygotes, being born as miniature versions of the adult, known as nymphs. The young moult three times before reaching the final adult form, which they usually reach within a month of hatching.

Ecology

Lice are optimal model organisms to study the ecology of contagious pathogens since their quantities, sex-ratios etc. are easier to quantify than those of other pathogens. The ecology of avian lice have been studied more intensively than that of mammal lice.

A few major trends

1. The average number of lice per host tends to be higher in large-bodied bird species than in small ones.
2. Louse individuals exhibit an aggregated distribution across bird individuals, i.e. most lice live on a few bird, while most birds are relatively free of lice. This pattern is more pronounced in territorial than in colonial – more social – bird species.
3. Host taxa that dive under the water surface to feed on aquatic prey harbour fewer taxa of lice.
4. Bird taxa that are capable to exert stronger antiparasitic defense – such as stronger T cell immune response or larger uropygial glands – harbour more taxa of Amblyceran lice than others.
5. Temporal bottlenecks in host population size may couse a long-lasting reduction of louse taxonomic richness. E.g., birds introduced into New Zealand host fewer species of lice there than in Europe.
6. Louse sex ratios are more balanced in more social hosts and more female-biased in less social hosts, presumably due to the stronger isolation among louse subpopulations (living on separate birds) in the latter case.

A few effects of lousiness upon the host

1. Lice may reduce host life expectancy.
2. Lice may transmit microbial diseases or helminth parasites.
3. Ischnoceran lice may reduce the thermoregulation effect of the plumage, thus heavily infected birds loss more heat than other ones.
4. Lousiness is a disadvantage in the context of sexual rivalry.

Classification

The order has traditionally been divided into two suborders, the sucking lice (Anoplura) and the chewing lice (Mallophaga); however, recent classifications suggest that the Mallophaga are paraphyletic and four suborders are now recognised:

- Anoplura: sucking lice, occurring on mammals exclusively
- Rhyncophthirina: parasites of elephants and warthogs
- Ischnocera: mostly avian chewing lice, however, one family parasitize mammals
- Amblycera: a primitive suborder of chewing lice, widspread on birds, however, also live on South-American And Australian mammals

It has been suggested that the order is contained by the Troctomorpha suborder of Psocoptera.

Lice in humans

Humans host three different kinds of lice: head lice, body lice , and pubic lice. Lice infestations can be controlled with lice combs, and medicated shampoos or washes. Adult and nymphal lice can survive on sheep-shearers' moccasins for up to 10 days, but microwaving the footwear for five minutes in a plastic bag will kill the lice.

Human lice and DNA discoveries

Lice have been the subject of significant DNA research that has led to discoveries on human evolution. For example, recent DNA evidence suggests that pubic lice spread to humans approximately 2,000,000 years ago from gorillas. Additionally, the DNA differences between head lice and body lice provide corroborating evidence that humans started losing body hair, also about 2,000,000 years ago.

Ricinus bombycillae, an Amblyceran louse from the bohemian waxwing

Trinoton anserinum, an Amblyceran louse from a mute swan.

Damalinia limbata is an Ischnoceran louse from goats. The male is smaller than the female.

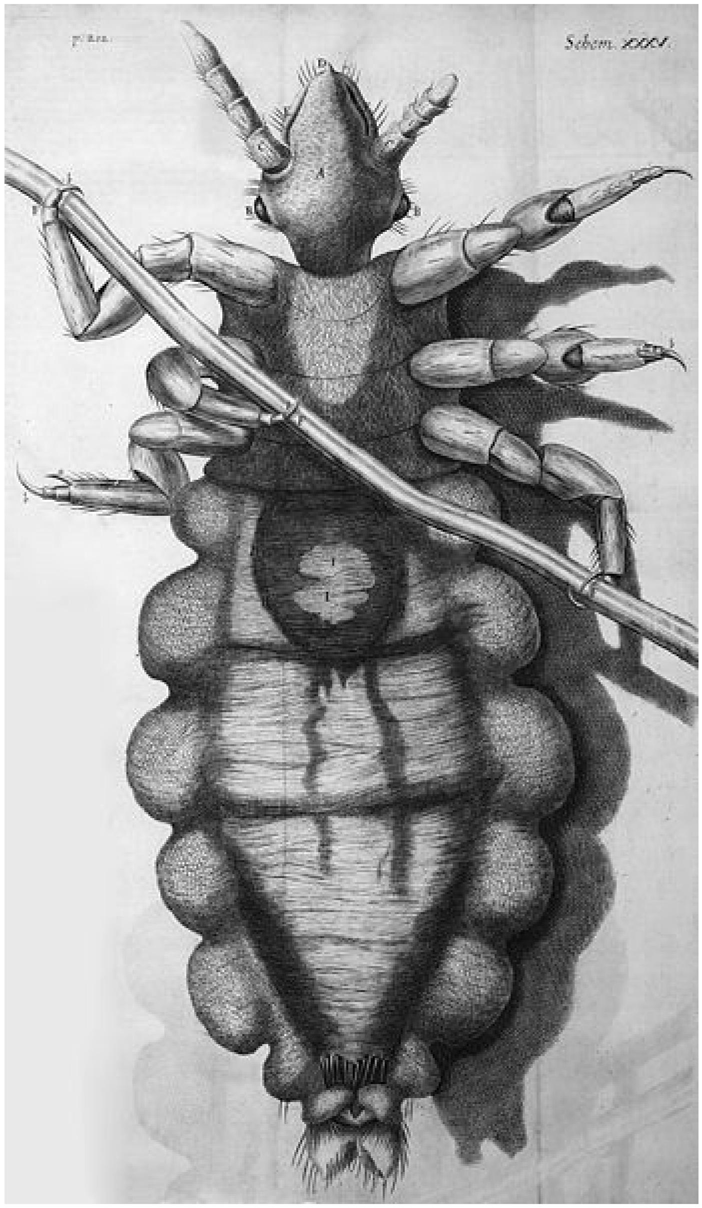


Diagram of a louse, by Robert Hooke, 1667.