Cambridge University Press
978-0-521-11389-2 - The Insects: Structure and Function: Fifth Edition
R. F. Chapman Edited by Stephen J. Simpson and Angela E. Douglas
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The Insects

Structure and Function

FIFTH EDITION

The Insects has been the standard textbook in the field since the first edition was published over 40 years ago. Building on the strengths of Chapman's original text, this long-awaited new edition has been revised and expanded by a team of eminent insect physiologists, bringing it fully up to date for the molecular era.

The chapters retain the successful structure of the earlier editions, focusing on particular functional systems rather than on taxonomic groups and making it easy for students to delve into topics without extensive knowledge of taxonomy. The focus is on form and function, bringing together basic anatomy and physiology and examining how these relate to behavior. This, combined with nearly 600 clear illustrations, provides a comprehensive understanding of how insects work.

Now also featuring a richly illustrated prologue by George McGavin, this is an essential text for students, researchers and applied entomologists alike.

R. F. Chapman (1930–2003) was an eminent insect physiologist and Professor in the Division of Neurobiology at the University of Arizona. His first four editions of *The Insects* have formed the standard text in the field for more than 40 years.

Stephen J. Simpson is ARC Laureate Fellow in the School of Biological Sciences and Academic Director of the Perkins Centre for the study of obesity, diabetes and cardiovascular disease at the University of Sydney. His core research aims are to understand swarming in locusts and to develop and implement an integrative framework for studying nutrition. In 2012 he was awarded the Wigglesworth Medal from the Royal Entomological Society of London.

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The Insects

Structure and Function

FIFTH EDITION

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Edited by

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PREFACE

Reginald Chapman's *The Insects: Structure and Function* has been the preeminent textbook for insect physiologists for the past 43 years (since the moon landing, in fact). For generations of students, teachers and researchers *The Insects* has provided the conceptual framework explaining how insects work. Without this book, the lives of entomologists worldwide would have been substantially more difficult. Nevertheless, the most recent (fourth) edition of this remarkable book was published in 1998, and a great deal has happened since then. Sadly, Reg died in 2003 and there was no reasonable prospect of any other person taking on the next revision single-handed. We have decided to take a different approach: to invite a team of eminent insect physiologists to bring their expertise to the collective enterprise of writing the fifth edition of *The Insects*.

Our aim has been to protect the identity of *The Insects* by working with Reg's original text. Certain areas have needed more revision than others, and some sections have been shrunk to accommodate advances in others. Our sole major deviation from the style of previous editions has been to remove all citations to primary literature from the main text. These in-text citations had accreted across successive revisions, and were somewhat patchy in coverage throughout the book. With the availability of online literature search engines today, students and researchers alike are better served by a short list of key references at the end of each chapter to provide a lead-in to the literature.

It has been the greatest pleasure for us to work with 23 colleagues from seven countries over the last four years, as the fifth edition of *The Insects* has taken shape. This project brings into sharp relief the intellectual strength and vigor of our discipline – the new discoveries over the last 14 years since the fourth edition are nothing short of breathtaking. We have also come to admire, more than ever, the breadth of Reg's knowledge and understanding of insects. He was a remarkable man.

STEVE SIMPSON and ANGELA DOUGLAS

ACKNOWLEDGMENTS

We wish to express our considerable gratitude to all our authors for their insight, expertise and commitment to this venture. We also thank Pedro Telleria-Teixeira for his tireless efforts in helping prepare the manuscript for submission, and to Cambridge University Press for taking it from there. Finally, we thank Elizabeth Bernays for her encouragement to take on the task. We hope that Reg would have been pleased with the result.

PROLOGUE

GEORGE C. McGAVIN

The ancestor of the Arthropoda was in all probability a segmented worm-like marine creature that lived in oceans during the late Precambrian. By the early to mid-Cambrian (540–520 million years ago) the early arthropods had already evolved into a range of clearly recognizable groups with distinct body plans. Arthropods are characterized by a number of features: the possession of a periodically molted, chitinous cuticle that acts as a rigid exoskeleton for the internal attachment of striated muscles; segmental paired legs; and the aggregation and/or fusing of body segments into discrete functional units, of which the most universal is the head. Besides the head there may be a trunk, as in the Myriapoda, or a separate thorax and abdomen as in the Crustacea and Hexapoda.

Based on the ubiquity of α-chitin in arthropod cuticles, similarities in musculature and tendon systems and recent molecular data, the overwhelming consensus of opinion is that this very large taxon is monophyletic. However, the relationships within the Arthropoda have been the subject of much controversy for more than 100 years. Recent molecular and genetic data confirm that the Hexapoda (comprising the Insecta and three other non-insect hexapod classes) are monophyletic, but that Crustacea are not. The monophyletic Hexapoda and paraphyletic Crustacea are now thought to form a single superclade called the Pancrustacea (Fig. 1). The mandibles of these two groups have similar origins, and the development of the nervous system is similar, as is the structure and wiring of the compound eyes.

A little over 1.5 million species of living organism have been scientifically described to date. The vast majority (66%) are arthropods such as crustaceans, arachnids, myriapods and insects. Insects represent 75% of all animals, and one insect order – the beetles (Coleoptera) – is famously species-rich, but another comprising the wasps, bees and ants (Hymenoptera) may rival the beetles if taxonomists ever complete their studies. One thing is clear, however – the full extent of Earth’s biodiversity remains a mystery. From attempts over 30 years ago to estimate the number of extant species to the present day we still only have a rough idea of how many species live alongside us. Estimates range from as few as five million to perhaps as many as 10–12 million species. The task of enumerating them may become substantially easier as the loss and degradation of natural habitats, especially the forests of the humid tropics, continues unabated. It is certain that the majority of insect species will become extinct before they are known to science.

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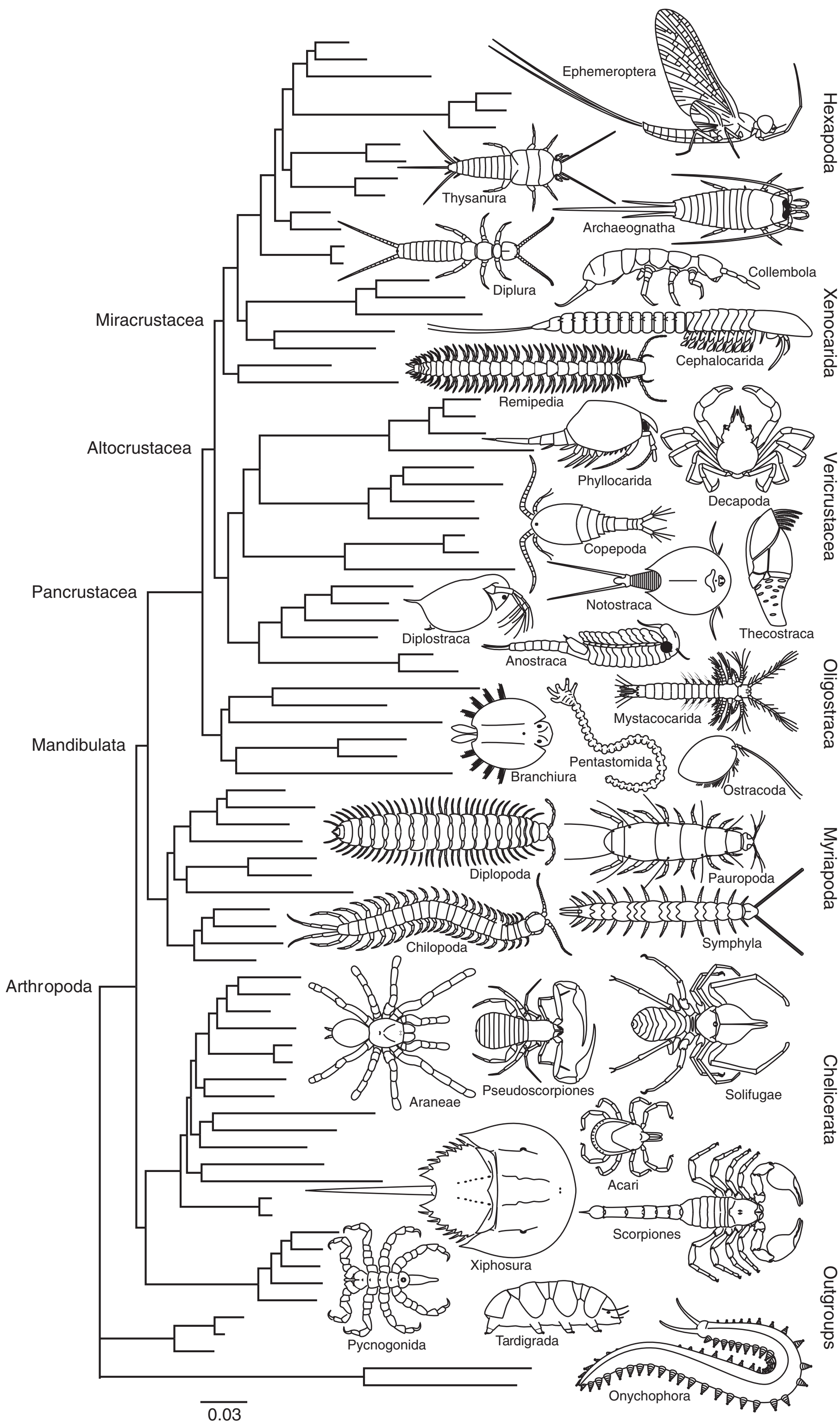


Figure 1 Phylogram of relationships for 75 arthropod and five outgroup species. Reprinted by permission from Macmillan Publishers Ltd: Regier, J. C., Shultz, J. W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J. W. and Cunningham, C. W. (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* 463, 1079–1083.

Insects are the dominant multicellular life form on the planet, ranging in size from minute parasitic wasps at around 0.2 mm to stick insects measuring 35 cm in length. Insects have evolved diverse lifestyles and although they are mainly terrestrial, there are a significant number of aquatic species. Insects have a versatile, lightweight and waterproof cuticle, are generally small in size and have a complex nervous system surrounded by an effective blood–brain barrier. Insects were the first creatures to take to the air and have prodigious reproductive rates. These factors, together with the complex interactions they have with other organisms, have led to their great success both in terms of species richness and abundance. The very high diversity of insects today is the result of a combination of high rates of speciation and the fact that many insect taxa are persistent – that is, they show relatively low rates of extinction.

In comparison to insects, vertebrate species make up less than 3% of all species. As herbivores they are altogether out-munched by the myriad herbivorous insects. In tropical forests, for example, 12–15% of the total leaf area is eaten by insects as compared with only 2–3% lost to vertebrate herbivores. Termites remove more plant material from the African savannahs than all the teeming herds of wildebeest and other ungulates put together. Vertebrates also fail to impress as predators. Ants are the major carnivores on the planet, devouring more animal tissue per annum than all the other carnivores. In many habitats ants make up one-quarter of the total animal biomass present.

Insects pollinate the vast majority of the world’s 250 000 or so species of flowering plant. The origin of bees coincides with the main radiation of the angiosperms approximately 100 million years ago, and without them there would be no flowers, fruit or vegetables. At least 25% of all insect species are parasites or predators of other insect species. Insects are also important in nutrient recycling by disposing of carcasses and dung.

Insects are the principal food source for many other animals. Virtually all birds and a large number of other vertebrates feed on them. An average brood of great tit chicks will consume around 120 000 caterpillars while they are in the nest and a single swallow chick may consume upwards of 200 000 bugs, flies and beetles before it fledges.

Insects can also have a huge negative impact on humans. One-sixth of all crops grown worldwide are lost to herbivorous insects and the plant diseases they transmit. About one in six human beings alive today is affected by an insect-borne illness such as plague, sleeping sickness, river blindness, yellow fever, filariasis and leishmaniasis. About 40% of the world’s population are at risk of malaria. More than 500 million people become severely ill and more than one million die from this disease every year. To complete the destructive side of their activities, insects can cause great damage to wooden structures and a wide range of natural materials and fabrics.

But without insects performing essential ecosystems services, the Earth would be a very different place and most terrestrial vertebrates that depend on them directly as food would become extinct. The loss of bees alone might cause the extinction of one-quarter of all life on Earth. A total loss of insects would see the human population plummet to perhaps a few hundred thousand individuals subsisting mainly on cereals.

Their small size and high reproductive rates make insects ideal model systems in molecular, cellular, organismal, ecological and evolutionary studies. Indeed, many of the most important discoveries in genetics, physiology, behavior, ecology and evolutionary biology have relied on insects.

There may come a day when humans venture far enough into space to visit other planets on which life has developed. If we do and there are multicellular organisms present, it is likely they will look a lot like insects.

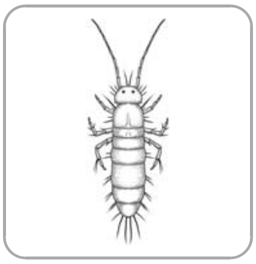
Mini-biographies of the insect orders

The Insecta and three other classes, the Protura, Diplura and Collembola, together comprise the arthropod superclass, Hexapoda. The Class Insecta is divided into 30 orders, which are outlined below.

THE PRIMITIVE WINGLESS INSECTS (INFRACLASS APTERYGOTA)

ARCHAEOGNATHA

- Bristletails
- ~500 species
- Body length: 7–15 mm



Bristletails are the most primitive living insects, having persisted for more than 400 million years. They are mainly nocturnal, living in leaf litter and under stones in a wide range of habitats from coastal to mountainous regions. The body, which is elongate with a cylindrical cross-section, is covered in tiny scales and has a characteristically humped thorax.

The head has a pair of long antennae, large contiguous compound eyes and three well-developed ocelli (single-faceted, simple eyes). The mouthparts are simple, with long maxillary palps. The mandibles have a single point of articulation (termed monocondylar) and are used to pick at lichens and algae. This jaw articulation is a very primitive feature separating the bristletails from all other insects, including the Thysanura, which have two points of articulation (dicondylar).

The abdomen has accessory walking appendages called styles (present on abdominal segments 2–9), which support the abdomen when bristletails run over uneven or steep surfaces. Surface water can be absorbed through one or two pairs of eversible vesicles located on the underside of abdominal segments 1–7. The abdomen has a pair of multi-segmented cerci and a much longer central filament. Bristletails can jump by rapid flexion of the abdomen.

THYSANURA (ZYGENTOMA)

- Silverfish
- <400 species
- Body length: 2–22 mm

Although very similar to bristletails, silverfish are actually more closely related to the winged insects. The body, which may have a covering of scales, is rather more flattened and the thorax is not humped. Silverfish are scavengers in soil, leaf litter, on trees and sometimes in buildings, where they can be minor pests.

The head has a pair of long antennae, small compound eyes and may have ocelli. The maxillary palps are shorter than those of the Archaeognatha and the jaws, although still of a primitive design, have two points of articulation and act in the transverse plane.

Styles may be present on abdominal segments 2–9, but usually on fewer segments (7–9). Pairs of water-absorbing, eversible vesicles usually occur on the abdominal segments (2–7), although in some species they are absent. The end of the abdomen has a pair of cerci and a central filament. Silverfish are fast running but do not jump.

THE WINGED INSECTS

The infraclass Pterygota is made up of three very unequal divisions. The mayflies (Ephemeroptera), comprising <0.3% of all insects species, and the dragonflies and damselflies (Odonata), comprising ~0.5% of all insect species, are each a division. Species in these two divisions are unable to fold their wings back along the body. Together they are sometimes termed the Paleoptera, although this is not a natural (monophyletic) grouping. The third, and by far the largest division, comprising all other insect species, is the Neoptera, which are monophyletic.

DIVISION I

EPHEMEROPTERA

- Mayflies
- ~2500 species
- Body length: 5–34 mm
- Wingspan: up to 50 mm

The Ephemeroptera are the oldest (basal) group of winged insects on Earth today and are unique in having a pre-adult winged stage called the subimago – they are the only insects that molt after they have developed functional wings. This habit was probably much more common in extinct Carboniferous and Permian taxa, where immature stages had wing-like structures and molted them throughout their lives.

The order is divided into two suborders, the Schistonota (split-back mayflies) and the Pannota (fused-back mayflies). Schistonotan nymphs have their wing pads free along the midline, whereas in pannotan nymphs, the wing pads are fused along the midline of the body.

Mayflies are soft-bodied with nearly cylindrical bodies, longish legs and typically two pairs of wings, which, when at rest, are held over the body. The head has a pair of short bristle-like antennae, a pair of large compound eyes and three ocelli. Adults have reduced non-functional mouthparts. The end of the abdomen bears a pair of elongate cerci and, usually, a single, long central filament.

The lifecycle is dominated by the aquatic, nymphal stages and adults live for a very short time, often less than a day.

DIVISION II

ODONATA

- Damselflies and dragonflies
- <6000 species
- Body length: up to 150 mm
- Wingspan: 18–200 mm

These fast-flying insects, often seen near water, are instantly recognizable. Odonates have a distinctive elongate body and are often brightly colored or metallic. They have a large, mobile head with very large compound eyes, three ocelli, short, hair-like antennae and biting mouthparts. They have two pairs of similarly sized wings, which can be used out of phase with each other, allowing great maneuverability.

The nymphal stages (called naiads) are aquatic and actively hunt or ambush prey. The mouthparts are unique in that there is a prehensile labial mask, which can be rapidly extended. Spine-like palps on the labium impale prey items and the mask is then folded back toward the mouth.

The order is split into two major suborders, the dragonflies (Anisoptera) and the damselflies (Zygoptera). A third suborder (Ansiozygoptera) comprises only two Oriental species. Dragonflies have round heads and very large eyes, while damselflies have broader heads with widely separated eyes. The large eyes give odonates near all-round vision and, as would be expected of aerial hunters, they are able to resolve distant objects better than any other insect.

DIVISION III: NEOPTERA

In all neopterans, flexor muscles attached to a third axillary sclerite at the base of the wings allow the wings to be folded back along the body. The evolution of a wing-folding mechanism allowed much better exploitation of the terrestrial environment without the risk of wing damage.

Subdivison: Hemimetabola

PLECOPTERA

- Stoneflies
- ~2000 species
- Body length: 3–48 mm
- Maximum wingspan: about 100 mm

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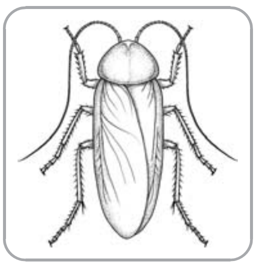
Stoneflies are slender insects with soft, slightly flattened bodies. The head has bulging eyes, two or three ocelli and thread-like antennae. The mouthparts are weakly developed or non-functional. They have two pairs of membranous wings, which are held flat or folded around the body at rest. They are not strong fliers and seldom travel far from water. The elongate abdomen has a pair of single- or multi-segmented cerci.

The order is divided into two suborders, the Arctoperlaria and the Antarctoperlaria. With the exception of one family, all Arctoperlaria are found in the Northern Hemisphere. All families in the Antarctoperlaria are found in the Southern Hemisphere.

Stonefly nymphs are aquatic and can swim using lateral body movements. Many graze algae from rocks.

BLATTODEA (BLATTARIA)



- Cockroaches
- ~4000 species
- Body length: 3–100 mm

Cockroaches are fast-running, flattened, broadly oval and leathery-bodied insects. The head, which is directed downwards and largely concealed by the pronotum, has biting mouthparts, well-developed compound eyes, two ocelli-like spots and long antennae. The front pairs of wings are toughened as protective "tegmina" to cover the larger, membranous hindwings. The abdomen carries a pair of one- or multi-segmented cerci. Eggs are typically laid in a toughened case or ootheca, a feature shared with the closely related, but entirely predatory Mantodea.

The vast majority of cockroaches are nocturnal, omnivorous or saprophagous species living in soil and leaf litter communities. Only about 40 species are considered pests because of their close association with humans, and only half of these have a significant impact. The main problem is that they can carry a huge diversity of pathogenic organisms on their tarsi and other body parts. When they feed they regurgitate partly digested food and leave behind their feces and a characteristic offensive odor. Exposure to high levels of cockroach allergens in house dust can produce serious health problems such as allergies, dermatitis, eczema and asthma.

MANTODEA

- Mantids
- ~2300 species
- Body length: 8–150 mm

These distinctive predatory insects have a triangular, highly mobile head with large compound eyes, thread-like antennae and usually three ocelli. The prothorax is typically elongate and carries the specialized, raptorial front legs. The front wings are narrow and toughened, protecting the much larger membranous hindwings. Eggs are laid in a papery, foam- or cellophane-like ootheca.

True binocular vision allows mantids to calculate the distance of their prey using triangulation. The coxa of the front legs is very elongate and the femur is enlarged and equipped with rows of sharp spines and teeth. The tibia, which is also spined or toothed, folds back on the inner face of the femur like a jack knife. The strike, which takes place in two phases, lasts less than 100 milliseconds. In the initial phase, the tibiae are fully extended in readiness for the second phase, which takes the form of a rapid sweeping action. The femora are quickly extended and, at the same time, the tibiae are flexed around the prey.

Mantids, which are mainly diurnal, predate a wide range of insects, spiders and other arthropods, which they ambush or stalk. Larger species have even been recorded catching and eating vertebrates such as frogs, mice and even small birds.

ISOPTERA

- Termites
- <3000 species
- Body length: 3–20 mm, mostly under 15 mm; queens can be up to 100 mm

Generally pale and soft-bodied, termites are social insects living in permanent colonies with different castes of both sexes. Workers and soldiers are wingless, while the reproductives (kings and queens) have two pairs of equal-sized wings, which are shed after a nuptial flight.

The foodstuff of termites, cellulose, is an abundant biomolecule but is difficult to break down. Termites have evolved symbiotic relationships with cellulase-producing microorganisms to make use of this resource. The gut of lower termites harbors protists, while those of the higher termites (Termitidae) contain bacterial symbionts.

Termites can build impressively large nest structures, including the large multi-vented chimneys that ventilate the subterranean nests of African *Macrotermes* species and the wedge-shaped nests in northern Australia made by the magnetic termite, *Amitermes meridionalis*.

Confined to regions between 45–50° north and south of the Equator, termites have an immense impact on soil enrichment and carbon cycling. They may consume up to one-third of the annual production of dead wood, leaves and grass and be present in huge numbers, comprising 10% of all animal biomass present.

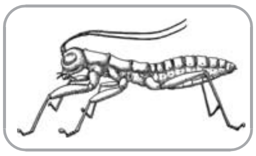
GRYLLOBLATTODEA (NOTOPTERA)

- Rock crawlers or ice crawlers
- 26 species (1 family: Grylloblattidae)
- Body length: 12–30 mm

These slender, wingless, slightly hairy insects were first discovered in the Canadian Rockies in 1913 and are a relict group confined to certain high-altitude regions across the Northern Hemisphere. The head has small compound eyes, although these are sometimes absent, no ocelli, slender, thread-like antennae and simple, chewing mouthparts. The abdomen is cylindrical, with a pair of slender, multi-segmented cerci.

Grylloblattids live under stones, decaying wood and leaf litter in cold temperate forests and sometimes in caves. There may be eight nymphal instars and complete nymphal development may take up to 5–6 years. As nymphs get older they become darker colored and add segments to their antennae at each molt. The adults typically live for less than two years.

MANTOPHASMATODEA



- Gladiators, African rock crawlers or heel-walkers
- 15 species (1 family: Mantophasmatidae)
- Body length: 12–35 mm

Discovered in 2002, the species that make up this small order live in dry, rocky habitats in southern Africa and may be related to the Grylloblattodea. The head has well-developed compound eyes and long, slender antennae and biting mouthparts, but lacks ocelli. The name "heel-walkers" refers to the way the claws are held clear of the ground when walking.

These elongate, wingless insects can be found under stone and among tufts of grasses and other plants. At night they emerge to catch other insects, holding small prey using their spiny front and middle legs.

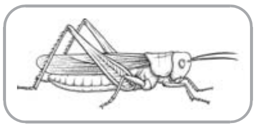
DERMAPTERA

- Earwigs
- ~1900 species
- Body length: 5–54 mm

Mostly drab, nocturnal and generally reluctant to fly, the majority of these elongate and slightly flattened insects are immediately recognizable on account of their distinctive abdominal forcep-like cerci. The head, which may have a pair of compound eyes but no ocelli, has biting mouthparts and long antennae. The front wings are short, leathery and veinless, covering the large, semicircular hindwings.

The order is divided into three very unequal suborders. The largest – which accounts for 99% of all known species – is the Forficulina, which prefer confined, humid microhabitats such as soil, leaf litter or beneath bark. The Hemimerina is made up of 11 species of African cockroach-like earwigs, which are ectoparasites in the fur of giant rats. The Arixenina comprises five blind, wingless South Asian species that feed on skin fragments and excreta in the fur or roosts of two species of molossid bat.

The terminal forceps, which are usually straight in females and curved in males, are used in a variety of ways but mainly as weapons for defense and prey handling, but also for courtship displays. The flexible and telescopic abdominal segments allow earwigs to use their forceps in all directions and they often use this ability to assist in folding the large hindwings.



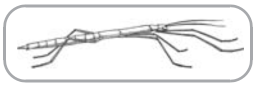
ORTHOPTERA

- Crickets, grasshoppers and relatives
- ~22 500 species
- Body length: 5–155 mm

These distinctive, elongate insects typically have enlarged hindlegs used for jumping. The head has well-developed compound eyes and may have ocelli. They have biting mouthparts and an enlarged, saddle- or shield-shaped pronotum. The front wings are toughened and typically narrower than hindwings, which are folded in longitudinal pleats beneath. The abdomen has a pair of short, terminal cerci.

The order is divided into two suborders, the Ensifera and the Caelifera. The Ensifera, comprising the crickets and katydids, have long or very long antennae and sing by rubbing structures on their front wings together. They are mainly nocturnal and solitary and most species mimic dead or living leaves. Many species are herbivorous, but some are partly or wholly predaceous. The ovipositor is always prominent and sword-, sickle- or stiletto-shaped.

The Caelifera, comprising grasshoppers and locusts (which show density-dependent polyphenism), have short antennae and the females never have prominent ovipositors. Songs are produced by a row of pegs on the hind femora rubbing against the edge of the front wings. They are generally ground-living, diurnal, grass- and/or forb-feeders and can be cryptically colored or brightly colored to advertise their unpalatability. Several, such as the desert locust, *Schistocerca gregaria*, are serious crop pests.



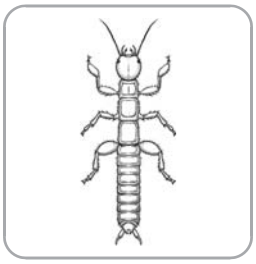
PHASMATODEA

- Stick and leaf insects
- >3000 species
- Body length: up to 566 mm, mostly 10–100 mm

The elongate body of stick insects can be short and smooth or large and very spiny or leaf-like. The head is characteristically domed and carries relatively long, thread-like antennae, chewing mouthparts, a pair of small compound eyes and, in winged species, ocelli. The front wings are short and toughened while the fan-shaped membranous hindwings are large. Many species are short-winged or wingless, and in others wing length varies between the sexes.

Stick insects are slow-moving, herbivorous and mostly nocturnal. Their shape and cryptic coloring make them very difficult to see among foliage and affords them protection from predators. Some species freeze motionless when disturbed, holding the middle and hindlegs along the body and stretching out the front legs, while others sway to imitate the movement of the vegetation. Leaf insects, which are broad and flattened with fantastic leaf-like expansions, are contained in one family, the Phylliidae, comprising about 50 species confined to Southeast Asia, New Guinea and Australia.

EMBIOPTERA (EMBIIDINA, EMBIODEA)

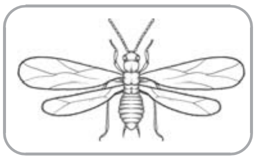


- Webspinners
- ~350 species
- Body length: 3–20 mm, mostly under 12 mm

Webspinners are narrow-bodied, cylindrical or slightly flattened gregarious insects living in warm temperate and tropical regions. The head has small, kidney-shaped compound eyes, thread-like antennae and biting mouthparts. The front legs of all life-stages and both sexes have swollen basal tarsal segments containing glands, which produce silk to make communal galleries in soil, litter and under bark.

As colonies grow, galleries and tunnels are extended to take in new food sources such as dead plant material, litter, lichens and mosses. Only adult females and nymphs feed. Males do not feed as adults and only use their jaws to grasp the female during copulation. Females are wingless but the males usually have two equal-sized pairs of long, narrow wings. The wings have hollow veins that can be inflated with hemolymph to make them stiff for flight. When the veins are not inflated, the wings can fold forwards without damage when the male has to run backwards through the galleries.

ZORAPTERA

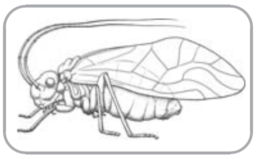


- Angel insects
- 32 species
- Body length: 2–3 mm

Mostly associated with rotting wood, these small, delicate-bodied insects are termite-like. The adults are dimorphic, being either blind, pale and wingless (resembling the nymphs) or darkly pigmented with eyes and two pairs of pale, sparsely veined wings. The head carries a pair of short, thread-like antennae and may have ocelli.

Zorapterans are gregarious under bark or in piles of wood dust, leaf litter or in termite nests, where they eat fungal threads, spores, mites and other small arthropods. As populations grow, winged morphs disperse to new locations and the wings are then shed. All the known species are currently assigned to a single genus, *Zorotypus*.

PSOCOPTERA



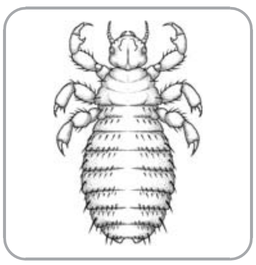
- Barklice and booklice
- <4500 species
- Body length: 1–10 mm, mostly under 6 mm

Barklice and booklice are very common insects, which on account of their small size and cryptic coloration, are often overlooked. The head is relatively large, with bulging compound eyes, long, thread-like antennae, biting mouthparts and, in winged species, three ocelli. The thorax is slightly humped and the wings, when present, are held roof-like over the body at rest.

Psocoptera can be found in a very wide range of terrestrial habitats, including caves and the nests of birds, bees and wasps, but are particularly abundant in litter and soil and on the bark and foliage of trees and shrubs. Most species graze on algae, lichens and molds and fungal spores, but some can be pests of stored products.

Three suborders are recognized – the Trogiomorpha, considered the most primitive, the Troctomorpha and the Psocomorpha, the most advanced suborder, containing more than 80% of the known species.

PHTHIRAPTERA



- Parasitic lice
- ~5000 species
- Body length: 1–10 mm, mostly under 6 mm

These small, wingless, dorso-ventrally flattened ectoparasites live permanently on bird or mammal hosts, where they feed on skin debris, secretions, feathers or blood.

The eyes are very small or absent, there are no ocelli and the antennae are short, with a maximum of five segments. The legs are short and robust, with the tarsi and claws typically modified for grasping hair or feathers. Several species are significant vectors of human and animal diseases.

The nymphs pass through three instars or nymphal stages, taking anything from two weeks to a few months to reach adulthood. Many lice have symbiotic relationships with bacteria which live in special mycetocytes associated with the digestive system. These bacteria allow the lice to digest feather protein (keratin) and blood.

There are four suborders within the Phthiraptera. The Amblycera are a primitive group of chewing lice living on birds and mammals. The Rhyncophthirina are ectoparasites of elephants and warthogs. The largest suborder, the Ischnocera, are chewing lice mainly found on birds, while the Anoplura are sucking lice which include the human head and body louse and the pubic louse.

HEMIPTERA

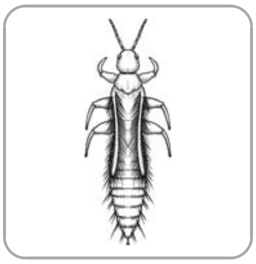
- True bugs
- >82 000 species
- Body length: 1–100 mm, mostly under 50 mm

True bugs range from minute, wingless scale insects to giant water bugs with raptorial front legs capable of catching fish and frogs. Compound eyes are often prominent and ocelli may be present. Bugs lack maxillary and labial palps and the mandibles and maxillae, which are enclosed by the labium, take the form of elongate, grooved stylets through which saliva can be injected and liquids sucked up. Two pairs of wings are usually present.

There are four distinct suborders. The Auchenorrhyncha, comprising planthoppers, leafhoppers, froghoppers, treehoppers, lantern bugs and cicadas, and the Sternorrhyncha, including jumping plant lice, whiteflies, phylloxerans, aphids and scale insects, are herbivorous. The Coleorrhyncha is represented by a single family of cryptic bugs found in the Southern Hemisphere. The majority of species belonging to the fourth suborder, the Heteroptera, are herbivorous but the suborder contains a significant number of predatory taxa and even some blood-sucking species. A characteristic feature of heteropterans is the possession of defensive stink glands.

Many bug species are significant plant pests and some transmit human and animal diseases.

THYSANOPTERA



- Thrips
- ~5500 species
- Body length: 0.5–12 mm, mostly under 3 mm

Thrips are small or very small, slender-bodied insects with prominent, large-faceted eyes, short antennae and asymmetrical piercing and sucking mouthparts. One mandible is very small and non-functional while the other is sharp and stylet-like and used to penetrate plant tissue or sometimes the bodies of minute insects. The other mouthparts form hemipteran-like stylets and are used to suck up liquid food. They usually have two pairs of very narrow, hair-fringed wings, but wings can be reduced, vestigial or absent. Three ocelli are present in winged individuals. The tarsi have an eversible bladder-like structure between the claws. Many species are serious plant pests.

Although these insects are most closely related to the Hemiptera, they are unusual in that there are one or more pupa-like resting stages between the two, true nymphal stages and the adult. In some cases there are three pre-adult stages of which the first may still be capable of feeding. The next two pre-adult stages become more pupa-like with a degree of tissue reorganization; a cocoon may even be formed.

Subdivison: Holometabola

The following neopteran orders comprise the most advanced and successful of all insects. The immature stages are called larvae and look very different and have different lifestyles to the adults. The wings develop internally and metamorphosis from larva to adult takes place during a pupal stage.

MEGALOPTERA

- Alderflies and dobsonflies
- ~300 species
- Body length: 10–150 mm
- Wingspan: 18–170 mm

The two families that comprise this small order (alderflies [Sialidae] and dobsonflies [Corydalidae]) are the most primitive insects with complete metamorphosis. The head has conspicuous compound eyes and long, thread-like antennae. Ocelli are present in corydalids but absent in sialids. Despite having well-developed jaws,

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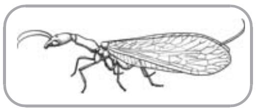
adult megalopterans do not feed. In some male dobsonflies the jaws may be several times the length of the head and used in male-to-male combat or for grasping the female. Megalopterans have two pairs of similarly sized wings, which are held roof-like over the body.

Megaloptera are found near cool, clean streams in temperate regions. Dobsonflies prefer running water while alderflies can be found in ponds and canals as well as streams. The predaceous larvae are aquatic with simple or branched, abdominal gills.

Larval development can take anything from 12 months in alderflies but sometimes more than 48 months in dobsonflies. Pupation takes place on land within a simple chamber made in moist soil, sand or mossy vegetation or under rotting wood. The pupae have functional jaws, can move around freely and even protect themselves.

RAPHIDIOPTERA

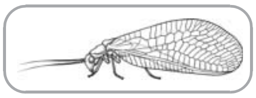


- Snakeflies
- ~220 species
- Body length: 6–28 mm

Confined to cool, temperate woodlands, this order comprises just two families, the Raphidiidae and the Inocellidae. The large head, which is supported by an elongate prothorax, is slightly flattened, broad in the middle and tapers to the rear. The antennae are slender and the compound eyes are conspicuous. Ocelli are present in the Raphidiidae but absent in the Inocellidae. The biting mouthparts are forward-facing to seize prey. The two pairs of wings are similarly sized, clear and have similar venation to that of megalopterans, but the veins are forked close to the wing margins as in neuropterans. Both pairs of wings have a small, dark or pale mark called the pterostigma on the front edge, toward the wing tips. The females, which are a little larger than males, have a long, slender and conspicuous ovipositor.

Snakeflies are closely related to alderflies but differ in that the larvae are completely terrestrial and the adult stage feeds.

NEUROPTERA



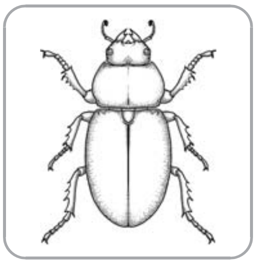
- Antlions, lacewings and relatives
- ~5000 species
- Body length: 2–90 mm
- Wingspan: 5–150 mm

Adult neuropterans have biting mouthparts, a pair of conspicuous, laterally placed compound eyes and may have ocelli. The antennae are generally long and thread-like, and in some owlflies and antlions the end of the antennae may be swollen to form a club. The adults of some families have prothoracic glands capable of producing substances that repel some predators. There are usually two pairs of similarly sized wings held roof-like over the body at rest. The venation in most neuropterans is net-like, with the main veins forking at the wing margins.

The majority of species are predatory and mainly active in the evening or after dark. The larvae of all species, which have their mandibles and maxillae united to form a pair of sharp, sucking tubes, are highly predaceous and can be found in a wide range of habitat types.

The species of some families are very similar to other insects. Adult Mantispidae have enlarged, raptorial front legs like those of praying mantids. Owlflies (Ascalaphidae) are aerial predators and look very like dragonflies.

COLEOPTERA



- Beetles
- ~370 000 species
- Body length: 0.1–180 mm, mostly under 25 mm

This very large order makes up at least 40% of all insect species.

The head has conspicuous compound eyes, antennae usually with less than 11 segments and biting mouthparts. Ocelli are typically absent. The prothorax is usually large and freely articulated with the rest of the thorax. The toughened front wings, or elytra, meet in the body midline and cover the larger membranous hindwings, which are folded lengthwise and crosswise underneath.

Beetles can be found in every conceivable terrestrial and freshwater habitat. The possession of protective elytra has allowed beetles to burrow, dig and squeeze into places that other insects cannot reach without compromising their ability to fly.

The order contains many scavengers, predators and a few specialized parasites, but the vast majority of beetle species are herbivorous and here lies the second major reason for their great success. The rise to dominance of the flowering plants (Angiospermae) in the Cretaceous provided herbivorous beetles with multiple opportunities to radiate.

The order is divided into four very unequal suborders. The Archostemata comprises a very small group of specialist wood-borers. The Mxyophaga is made up of around 60 species of small aquatic species. The Adephaga, comprising about 10% of all beetles, is made up of 12 families of ground-living and aquatic species where the larvae and adults are predaceous. The species that make up the largest suborder, the Polyphaga, have very diverse lifestyles and eating habits.

STREPSIPTERA

- Strepsipterans
- ~600 species
- Body length: 0.4–35 mm, mostly under 6 mm

Strepsipterans are highly specialized endoparasites of other insects in more than 30 insect families belonging to the Orders Thysanura, Blattodea, Mantodea, Orthoptera, Hemiptera, Diptera and Hymenoptera. The adults are dimorphic. Females are typically endoparasitic without eyes, antennae, mouthparts, legs or

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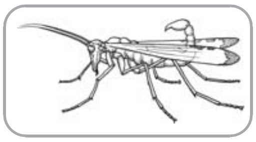
wings. Males are free-living, with raspberry-like eyes, branched antennae and wings. The front wings are small and strap-like while the hindwings are fan-shaped.

The order is divided into two suborders, the Mengenillidia (one small family – the Mengenillidae) and the Stylopidia (seven families). In the Mengenillidae, full-grown male and female larvae leave the hosts, which are species of silverfish, and pupation takes places outside. In this family, unusually, both adult males and females are free-living, but the females are not grub-like and have normal features of adult insects, such as legs and antennae. Females of all other families are totally endoparasitic. They never leave the confines of their host's body and are surrounded by the cuticle of their own pupal stage.

MECOPTERA

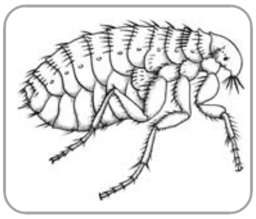


- Scorpionflies
- ~600 species
- Body length: 3–28 mm

Scorpionflies are elongate insects found mostly in damp woodlands. The head, which is characteristically extended downwards to form a beak, has biting mouthparts, slender, thread-like antennae, large compound eyes and three ocelli. They usually have two pairs of large, narrow wings, but some species are short-winged or wingless.

The legs are long and slender in most species, but in the hangingflies (Bittacidae) they are very long and used for prey capture. The fifth tarsal segment of the hindlegs is enlarged and raptorial to seize small insects. The majority of other scorpionflies feed on dead or dying insects and will also feed on carrion, nectar, sap and fruit juices.

SIPHONAPTERA



- Fleas
- ~2500 species
- Body length: 1–8 mm, mostly under 5 mm

Found wherever there are suitable hosts, fleas are a distinctive and readily recognizable group. Well over 90% of flea species feed on the blood of land mammals – the remainder are bird ectoparasites. Fleas are small, wingless, tough-bodied and laterally flattened. The head typically has very short, three-segmented antennae, which fit into grooves and short mouthparts for piercing skin and sucking blood. Fleas may have a pair of simple, lateral eyes similar to ocelli, and are negatively phototactic (avoid light). The enlarged hindlegs are part of the flea's unique and powerful jumping mechanism, which incorporates an energy store made of a rubber-like protein called resilin.

Comb-like structures on the cheeks and the posterior edge of the pronotum of many species, together with numerous backward-pointing spines and bristles on the body, help the fleas to remain in the host's fur. As holometabolous insects, the larvae are very different from the adults and feed on detritus and dried blood in the host's lair or den. Pupation takes place inside a loose cocoon. Many flea species are disease vectors.

DIPTERA

- True flies
- ~122 000 species
- Body length: 0.5–60 mm
- Wingspan: up to 75 mm

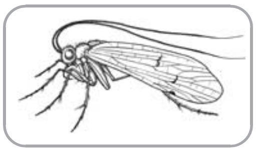
Most of the species that make up this huge and diverse order are beneficial to ecosystem function as pollinators, parasites and predators, and are vital to the processes of decomposition and nutrient recycling. However, the activities of relatively few species have a greater impact on man and other animals than any other insect group. Perhaps as many as one person in six is affected by a fly-borne disease such as malaria, yellow fever, dengue fever and leishmaniasis.

Flies have a mobile head with large compound eyes and three ocelli. The mouthparts, which vary according to diet, are adapted for lapping and sponging liquids or piercing and sucking.

A characteristic feature of the order is the possession of a single pair of membranous front wings, although some ectoparasitic species are wingless. The hindwings in all species are reduced to form a pair of balancing organs called halteres.

The order is divided into two suborders, the Nematocera and the Brachycera. Nematocera is the more primitive suborder, and includes crane flies, mosquitoes, black flies, midges and fungus gnats, with delicate thread-like antennae. The Brachycera are more robust, with short, stout antennae of less than six segments, and include the orthorrhaphan groups, typified by horse flies and robber flies, and the cyclorrhaphan species such as fruit flies, hover flies, blowflies and flesh flies. Larval habits vary from fully aquatic to terrestrial and many larvae are serious plant pests.

TRICHOPTERA



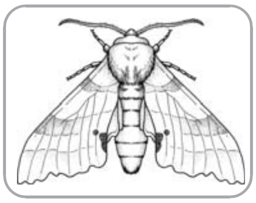
- Caddis flies
- >11 000 species
- Body length: 2–38 mm

Caddis flies are mainly nocturnal and can be found almost everywhere there is freshwater. The elongate adults are rather moth-like in appearance with long, slender legs. The body and wings, particularly the front wings, are covered with hairs. The head has a pair of large compound eyes, long, thin antennae and two or three ocelli may be present. The weakly developed mouthparts allow adults to lick up water and nectar, but many do not feed as adults. The front and hind pairs of wings are held over the body in a characteristically tent-like manner.

The caterpillar-like larvae, which are aquatic, show a range of feeding habits. Some species may be free-living or spin food-catching nets, but most live inside portable tube-like cases made from sand grains, small stones or bits of vegetation held together with silk secreted from glands in the head.

The order, which is most closely related to the Lepidoptera, is divided into two suborders, the Annulipalpia, mostly with net-spinning larvae, and the Integripalpia, comprised of species with mostly tube-case-building larvae.

LEPIDOPTERA



- Butterflies and moths
- ~200 000 species
- Wingspan: 3–300 mm, mostly under 75 mm

Members of this readily recognizable order occur everywhere there is vegetation. The body and wings of these familiar insects are covered with minute scales, which may be colored or iridescent. The compound eyes are large and the mouthparts typically take the form of a coiled proboscis through which liquids such as nectar can be sucked. The larvae, known as caterpillars, are typically herbivorous and have a number of abdominal prolegs in addition to the three pairs of thoracic legs. When fully grown they spin a silk cocoon in which they pupate. Some species are significant plant pests.

The order is divided into four suborders, three of them – the Zeugloptera (one family – Micropterigidae), the Aglossata (one family – Agathiphagidae) and Heterobathmiina (one family – Heterobathmiidae) – with only a handful of species. The fourth – Glossata – contains the vast majority of the species. Within the Glossata, the superfamily Papilionoidea comprises the four true butterfly families, the Papilionidae, Pieridae, Lycaenidae and Nymphalidae.

The first Lepidoptera appeared in the Jurassic and then radiated greatly with the rise of flowering plants in the Cretaceous.

HYMENOPTERA

- Sawflies, wasps, bees and ants
- >150 000 species
- Body length: 0.25–70 mm

Abundant and ubiquitous, it is almost certain that the true number of living species of Hymenoptera may exceed 500 000. Species within the order exhibit an incredible diversity of lifestyles: solitary or social, herbivorous, carnivorous or parasitic. The Hymenoptera must be regarded as the most beneficial of all insects for the control of natural insect populations exerted by parasitic and predatory wasp species and the pollination services of bees.

The head carries a pair of thread-like antennae, a pair of well-developed compound eyes and, usually, three ocelli. The mouthparts are adapted for chewing and biting but, in many species, liquids are ingested. In the bees (superfamily