Subphylums of Arthropoda

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Phylum:	Arthropoda
Subphylum:	**Chelicerata** Heymons, 1901
Classes	

- Arachnida
- Pycnogonida
- Merostomata

The subphylum constitutes one of the major subdivisions of the phylum (or superphylum) Arthropoda, and includes horseshoe crabs, scorpions, spiders and mites. They originated as marine animals, possibly in the Cambrian period, but the first confirmed chelicerate fossils, eurypterids, date from 445 million years ago in the Late Ordovician period. The surviving marine species include the four species of Xiphosurans (horseshoe crabs), and possibly the 1,300 species of Pycnogonida (sea spiders), if the latter are chelicerates. On the other hand, there are over 77,000 well-identified species of air-breathing chelicerates, and there may be about 500,000 unidentified species.

Like all arthropods, chelicerates have segmented bodies with jointed limbs, all covered in a cuticle made of chitin and proteins. The chelicerate bauplan consists of two tagmata, the cephalothorax and the abdomen, except that mites have lost a visible division between these sections. The chelicerae, which give the group its name, are the only appendages that appear before the mouth. In most sub-groups they are modest pincers used in feeding. However, spiders' chelicerae form fangs which in most species are used to inject venom into their prey. The group has the open circulatory system typical of the arthropods, in which a tube-like heart pumps blood through the hemocoel, which is the major body cavity. Marine chelicerates have gills, while the air-breathing forms generally have both book lungs and tracheae. In general the ganglia of living chelicerates' central nervous systems fuse into large masses in the cephalothorax, but there are wide variations and this fusion is very limited in the Mesothelae, which are regarded as the oldest and most primitive group of spiders. Most chelicerates rely on modified bristles for touch and for information about vibrations, air currents, and chemical changes in their environment. The most active hunting spiders also have very acute eyesight.

Chelicerates were originally predators, but the group has diversified to use all the major feeding strategies: predation, parasitism, herbivory, scavenging and eating decaying organic matter. Although harvestmen can digest solid food, the guts of most modern chelicerates are too narrow for this, and they generally liquidize their food by grinding it with their chelicerae and pedipalps and flooding it with digestive enzymes. To conserve water, air-breathing chelicerates excrete waste as solids that are removed from their blood by Malpighian tubules, structures which also evolved independently in insects. While the marine horseshoe crabs rely on external fertilization, air-breathing chelicerates use internal but usually indirect fertilization. Predatory species generally use elaborate courtship rituals to prevent males from being eaten before they can mate. Most lay eggs that hatch as what look like miniature adults, but all scorpions and a few species of mites keep the eggs inside their bodies until the young emerge. In most chelicerate species the young have to fend for themselves, but in scorpions and some species of spider the females protect and feed their young.

The evolutionary origins of chelicerates from the early arthropods have been debated for decades. Although there is considerable agreement about the relationships between most chelicerate sub-groups, the inclusion of the Pycnogonida in this taxon has recently been questioned (see below), and the exact position of scorpions is still controversial, though they were long considered the most primitive (basal) of the arachnids.

Although the venom of a few spider and scorpion species can be very dangerous to humans, medical researchers are investigating the use of these venoms for the treatment of disorders ranging from cancer to erectile dysfunction. The medical industry also uses the blood of horseshoe crabs as a test for the presence of contaminant bacteria. Genetic engineers have experimented with modifying goats' milk and plants' leaves to produce spider silk. Mites can cause allergies in humans, transmit several diseases to humans and their livestock, and are serious agricultural pests.

Description

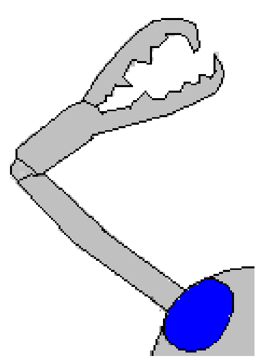
Segmentation and cuticle

The Chelicerata are arthropods as they have: segmented bodies with jointed limbs, all covered in a cuticle made of chitin and proteins; heads that are composed of several segments that fuse during the development of the embryo; a much reduced coelom; a hemocoel through which the blood circulates, driven by a tube-like heart. Chelicerates' bodies consist of two tagmata, sets of segments that serve similar functions: the foremost one, called the cephalothorax or prosoma, is a complete fusion of the segments that in an insect would form two separate tagmata, the head and thorax; the rear tagma is called the abdomen or opisthosoma. However in the Acari (mites and ticks) there is no visible division between these sections.

The cephalothorax is formed in the embryo by fusion of the acron, which carries the eyes, with segments two to seven, which all have paired appendages, while segment one is lost during the embryo's development. Segment two has a pair of chelicerae, small appendages that often form pincers, segment three has a pair of pedipalps that in most sub-groups perform sensory functions, while the remaining four cephalothorax segments have pairs of legs. In primitive forms the acron has a pair of compound eyes on the sides and four pigment-cup ocelli ("little eyes") in the middle. The mouth is between segments two and three.

The abdomen consists of twelve or fewer segments which originally formed two groups, a "preabdomen" or "mesoma" of seven segments and a "postabdomen" or "metasoma" of five, terminating with a telson or spike. The abdominal appendages of modern chelicerates are missing or heavily modified – for example in spiders the remaining appendages form spinnerets that extrude silk, while those of horseshoe crabs (Xiphosura) form gills.

Like all arthropods, chelicerates' bodies and appendages are covered with a tough cuticle made mainly of chitin and proteins which are chemically hardened. Since this cannot stretch, the animals have to molt in order to grow, in other words they grow new but still soft cuticles and then cast off the old one and wait for the new one to harden. Until the new cuticle has hardened the animals are defenseless and almost immobilized.



The chelicera of a eurypterid.

Spider's chelicera, showing the fang almost completely folded away.

Chelicerae and pedipalps

These appendages vary widely in form and function and the only consistent difference between them is their position: chelicerae arise from segment two, ahead of the mouth, and pedipalps from segment three, behind the mouth.

The chelicerae ("claw horns") that give the sub-phylum its name normally consist of three sections, and the claw is formed by the third section and a rigid extension of the second. However spiders' have only two sections, and the second forms a fang that folds away behind the first when not in use. The relative sizes of chelicerae vary widely: those of some eurypterids formed large claws that extended ahead of the body, while scorpions' are tiny pincers that are used in feeding and project only slightly in front of the head.

In most chelicerates the pedipalps are relatively small and are used as sensors. However those of male spiders have bulbous tips that act as syringes to inject sperm into the females' reproductive openings when mating, while scorpions' form large claws used for capturing prey.

Body cavities and circulatory systems

As in all arthropods, the chelicerate body has a very small coelom restricted to small areas round the reproductive and excretory systems. The main body cavity is a hemocoel that runs most of the length of the body and through which blood flows, driven by a tubular heart that collects blood from the rear and pumps it forward. Although arteries direct the blood to specific parts of the body, they have open ends rather than joining directly to veins, and chelicerates therefore have open circulatory systems as is typical for arthropods.

Respiratory systems

These depend on individual sub-groups' environments. Modern terrestrial chelicerates generally have both book lungs, which deliver oxygen and remove waste gases via the blood, and tracheae, which do the same without using the blood as a transport system. The living horseshoe crabs are aquatic and have book gills that lie in a horizontal plane. For a long time it was assumed that the extinct eurypterids had gills, but the fossil evidence was ambiguous. However a fossil of the 45 millimetres (1.8 in) long eurypterid *Onychopterella*, from the Late Ordovician period, has what appear to be three pairs of vertically-oriented book gills whose internal structure is very similar to that of scorpions' book lungs.

Feeding and digestion

The guts of most modern chelicerates are too narrow to take solid food. All scorpions and almost all spiders are predators that "pre-process" food in preoral cavities formed by the chelicerae and the bases of the pedipalps. However one predominantly vegetarian spider species is known, and many supplement their diets with nectar and pollen. Many of the Acari (ticks and mites) are blood-sucking parasites, but there are many predatory, vegetarian and scavenger sub-groups. All the Acari have a retractable feeding assembly that consists of the chelicerae, pedipalps and parts of the exoskeleton, and which forms a preoral cavity for pre-processing food.

Harvestmen are among the minority of living chelicerates that can take solid food, and the group includes predators, vegetarians and scavengers. Horseshoe crabs are also capable of processing solid food, and use a distinctive feeding system. Claws at the tips of their legs grab small invertebrates and pass them to a food groove that runs from between the rearmost legs to the mouth, which is on the underside of the head and faces slightly backwards. The bases of the legs form toothed gnathobases that both grind the food and push it towards the mouth. This is how the earliest arthropods are thought to have fed.

Excretion

Horseshoe crabs convert nitrogenous wastes to ammonia and dump it via their gills, and excrete other wastes as feces via the anus. They also have nephridia ("little kidneys"), which extract other wastes for excretion as urine. Ammonia is so toxic that it must be diluted rapidly with large quantities of water. Most terrestrial chelicerates cannot afford to use so much water and therefore convert nitrogenous wastes to other chemicals which can be excreted as dry matter. Extraction is done by various combinations of nephridia and Malpighian tubules. The tubules filter wastes out of the blood and dump them into the hindgut as solids, a system that has evolved independently in insects and several groups of arachnids.

Nervous system

	Cephalothorax ganglia fused into brain	Abdominal ganglia fused into brain
Horseshoe crabs	All	First two segments only
Scorpions	All	None
Mesothelae	First two pairs	None

	only	
Other arachnids	All	All

Chelicerate nervous systems are based on the standard arthropod model of a pair of nerve cords, each with a ganglion per segment, and a brain formed by fusion of the ganglia just behind the mouth with those ahead of it. However since chelicerates lose the first segment, which bears antennae in other arthropods, chelicerate brains include only one pair of pre-oral ganglia instead of two. There is a notable but variable trend towards fusion of other ganglia into the brain. The brains of horseshoe crabs include all the ganglia of the cephalothorax plus those of the first two abdominal segments, while the other abdominal segments retain separate pairs of ganglia. In most living arachnids, except scorpions if they are true arachnids, *all* the ganglia, including those which would normally be in the abdomen, are fused into a single mass in the cephalothorax and there are no ganglia in the abdomen. However in the Mesothelae, which are regarded as the most primitive living spiders, the ganglia of the abdomen and the rear part of the cephalothorax remain unfused, and in scorpions the ganglia of the cephalothorax are fused but the abdomen retains separate pairs of ganglia.

Senses

As with other arthropods, chelicerates' cuticles would block out information about the outside world, except that they are penetrated by many sensors or connections from sensors to the nervous system. In fact spiders and other arthropods have modified their cuticles into elaborate arrays of sensors. Various touch and vibration sensors, mostly bristles called setae, respond to different levels of force, from strong contact to very weak air currents. Chemical sensors provide equivalents of taste and smell, often by means of setae.

Living chelicerates have both compound eyes, mounted on the sides of the head, and pigment-cup ocelli ("little eyes"), mounted in the middle. The eyes of horseshoe crabs can detect movement but not form images. At the other extreme, jumping spiders have a very wide field of vision, and their main eyes are ten times as acute as those of dragonflies.

Reproduction

Female scorpion *Compsobuthus werneri* carrying its young (white)

Horseshoe crabs, which are aquatic, use external fertilization, in other words the sperm and ova meet outside the parents' bodies. Their trilobite-like larvae look rather like miniature adults as they have full sets of appendages and eyes, but initially they have only two pairs of book-gills and gain three more pairs as they molt.

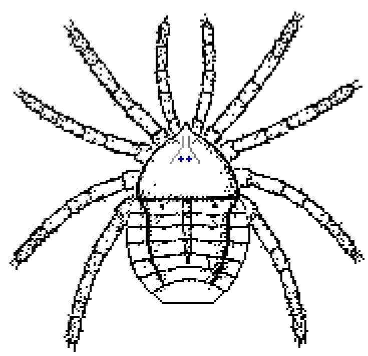
Being air-breathing animals, the living arachnids use internal fertilization, which is direct in some species, in other words the males' genitalia make contact with the females'. However in most species fertilization is indirect. Male spiders use their pedipalps as syringes to "inject" sperm into the females' reproductive openings, but most arachnids produce spermatophores (packages of sperm) which the females take into their bodies. Courtship rituals are common, especially in the most powerful predators, where males risk being eaten before mating. Most arachnids lay eggs, but all scorpions and a few mites keep the eggs inside their bodies until they hatch and offspring rather like miniature adults emerge.

Levels of parental care for the young range from zero to prolonged. Scorpions carry their young on their backs until the first molt, and in a few semi-social species the young remain with their mother. Some spiders care for their young, for example a wolf spider's brood cling to rough bristles on the mother's back, and females of some species respond to the "begging" behavior of their young by giving them their prey, provided it is no longer struggling, or even regurgitate food.

Evolutionary history

Fossil record

There are large gaps in the chelicerates' fossil record because, like all arthropods, their exoskeletons are organic and hence their fossils are rare except in a few lagerstätten where conditions were exceptionally suited to preserving fairly soft tissues. The Burgess shale animals *Sanctacaris* and *Sidneyia* from about 505 million years ago have been classified as chelicerates, the former because of its pattern of tagmosis (how the segments are grouped, especially in the head) and the latter because its appendages resemble those of the Xiphosura (horseshoe crabs). However cladistic analyses that consider wider ranges of characteristics place neither as chelicerates. There is debate about whether *Fuxianhuia* from earlier in the Cambrian period, about 525 million years ago, was a chelicerate. Another Cambrian fossil, *Kodymirus*, was originally classified as an aglaspid but may have been a eurypterid and therefore a chelicerate. If any of these was closely related to chelicerates, there is a gap of at least 43 million years in the record between true chelicerates and their nearest not-quite chelicerate relatives.



Palaeotarbus jerami, a trigonotarbid and the oldest known arachnid

Until recently the earliest known xiphosuran fossil dated from the Late Llandovery stage of the Silurian 436 to 428 million years ago, but in 2008 an older specimen was reported from about 445 million years ago in the Late Ordovician. Eurypterids have left few good fossils and the earliest confirmed eurypterids appear in the Late Ordovician period a little over 445 million years ago.

The oldest known arachnid is the trigonotarbid *Palaeotarbus jerami*, from about 420 million years ago in the Silurian period, and had a triangular cephalothorax and segmented abdomen, as well as eight legs and a pair of pedipalps.

Attercopus fimbriunguis, from 386 million years ago in the Devonian period, bears the earliest known silk-producing spigots, and was therefore hailed as a spider, but it lacked spinnerets and hence was not a true spider. Several Carboniferous spiders were members of the Mesothelae, a primitive group now represented only by the Liphistiidae.

The Late Silurian *Proscorpius* has been classified as a scorpion, but differed significantly from modern scorpions: it appears wholly aquatic since it had gills rather than book lungs or tracheae; its mouth was completely under its head and almost between the first pair of legs, as in the extinct eurypterids and living horseshoe crabs. Fossils of terrestrial scorpions with book lungs have been found in Early Devonian rocks form about 402 million years ago.

Relationships with other arthropods

The "traditional" view of the arthropod "family tree" shows chelicerates as less closely related to the other major living groups (crustaceans; hexapods, which includes insects; and myriapods, which includes centipedes and millipedes) than these other groups are to each other. Recent research since 2001, using both molecular phylogenetics (the application of cladistic analysis to biochemistry, especially to organisms' DNA and RNA) and detailed examination of how various arthropods' nervous systems develop in the embryos, suggests that chelicerates are most closely related to myriapods, while hexapods and crustaceans are each other's closest relatives. However these results are derived from analyzing only living arthropods, and including extinct ones such as trilobites causes a swing back to the "traditional" view, placing trilobites as the sister-group of the Tracheata (hexapods plus myriapods) and chelicerates as least closely related to the other groups.

Major sub-groups

It is generally agreed that the Chelicerata contain the classes Arachnida (spiders, scorpions, mites, etc.), Xiphosura (horseshoe crabs) and Eurypterida (sea scorpions, extinct). The extinct Chasmataspida may be a sub-group within Eurypterida. The Pycnogonida (sea spiders) were traditionally classified as chelicerates, but some features suggest they may be representatives of the earliest arthropods from which the well-known groups such as chelicerates evolved.

However the structure of "family tree" relationships within the Chelicerata has been controversial ever since the late 19th century. An attempt in 2002 to combine analysis of RNA features of modern chelicerates and anatomical features of modern and fossil ones produced credible results for many lower-level groups, but its results for the high-level relationships between major sub-groups of chelicerates were unstable, in other words minor changes in the inputs caused significant changes in the outputs of the computer program used (POY). An analysis in 2007 using only anatomical features produced the cladogram on the right, but also noted that many uncertainties remain.

The position of scorpions is particularly controversial. Some early fossils such as the Late Silurian *Proscorpius* have been classified by paleontologists as scorpions, but described as wholly aquatic as they had gills rather than book lungs or tracheae. Their mouths are also completely under their heads and almost between the first pair of legs, as in the extinct eurypterids and living horseshoe crabs. This presents a difficult choice: classify *Proscorpius* and other aquatic fossils as something other than scorpions, despite the similarities; accept that "scorpions" are not monophyletic but consist of separate aquatic and terrestrial groups; or treat scorpions as more closely related to eurypterids and possibly horseshoe crabs than to spiders and other arachnids, so that either scorpions are not arachnids or "arachnids" are not monophyletic.

Diversity

Although well behind the insects, chelicerates are one of the most diverse groups of animals, with over 77,000 living species that have been described in scientific publications. Some estimates suggest that there may be 130,000 undescribed species of spider and nearly 500,000 undescribed species of mites and ticks. While the earliest chelicerates and the living Pycnogonida (if they are chelicerates) and Xiphosura are marine animals that breathe dissolved oxygen, the vast majority of living species are air-breathers, although a few spider species build "diving bell" webs that enable them to live under water. Like their ancestors, most living chelicerates are carnivores, mainly on small invertebrates. However many species feed as parasites, vegetarians, scavengers and detritivores.

Diversity of living chelicerates

Group	Described species	Diet
Pycnogonida (sea-spiders)	500	Carnivorous
Xiphosura (horseshoe crabs)	4	Carnivorous
Araneae (spiders)	34,000	Carnivorous; 1 vegetarian
Acari (mites and ticks)	32,000	Carnivorous, parasitic, vegetarian, detritivore
Opiliones (harvestmen)	5,000	Carnivorous, vegetarian, detritivore
Pseudoscorpiones (false scorpions)	3,200	Carnivorous
Scorpiones (scorpions)	1,400	Carnivorous
Solifugae (sunspiders)	900	Carnivorous, omnivorous
Schizomida (small whipscorpions)	180	
Amblypygi (whipspiders)	100	
Uropygi (Thelyphonida – whipscorpions)	90	Carnivorous
Palpigradi (micro whipscorpions)	60	
Ricinulei	60	

Interaction with humans

A microscopic mite *Lorryia formosa*.

In the past, Native Americans ate the flesh of horseshoe crabs, and used the tail spines as spear tips and the shells to bail water out of their canoes. More recent attempts to use horseshoe crabs as food for livestock were abandoned when it was found that this gave the meat a bad taste. The blood of horseshoe crabs contains a clotting agent Limulus Amebocyte Lysate which is now used to test that antibiotics and kidney machines are free of dangerous bacteria, and to detect spinal meningitis and some cancers.

Cooked tarantula spiders are considered a delicacy in Cambodia, and by the Piaroa Indians of southern Venezuela. Spider venoms may be a less polluting alternative to conventional pesticides as they are deadly to insects but the great majority are harmless to vertebrates. Possible medical uses for spider venoms are being investigated, for the treatment of cardiac arrhythmia, Alzheimer's disease, strokes, and erectile dysfunction. Because spider silk is both light and very strong, attempts are being made to produce it in goats' milk and in the leaves of plants, by means of genetic engineering. There were about 100 reliably reported deaths from spider bites in the 20th century, compared with 1,500 from jellyfish stings.

Scorpion stings are thought to be a significant danger in less-developed countries, for example they cause about 1,000 deaths per year in Mexico but only one every few years in the USA. Most of these incidents are caused by accidental human "invasions" of scorpion's nests. However medical uses of scorpion venom are being investigated for treatment of brain cancers and bone diseases.

Ticks are parasitic, and some transmit micro-organisms and parasites that can cause diseases in humans, while the saliva of a few species can directly cause tick paralysis if they are not removed within a day or two.

A few of the closely-related mites also infest humans, some causing intense itching by their bites and others by burrowing into the skin. Species that normally infest other animals such as rodents may infest humans if their normal hosts are eliminated. Three species of mite are a threat to honey bees and one of these, *Varroa destructor*, has become the largest single problem faced by beekeepers worldwide. Mites cause several forms of allergic diseases, including hay fever, asthma and eczema, and they aggravate atopic dermatitis. Mites are also significant crop pests, although predatory mites may be useful in controlling some of these.

Chapter 2

Myriapoda and Hexapoda

Myriapoda

Myriapoda Temporal range: Late Silurian–Recent	

Lithobius forficatus, a centipede

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	**Myriapoda** Latreille, 1802

Classes

- Chilopoda
- Diplopoda
- Pauropoda
- Symphyla
- Arthropleuridea (extinct)

Myriapoda is a subphylum of arthropods containing millipedes, centipedes, and others. The group contains 13,000 species, all of which are terrestrial. Although their name suggests they have myriad (10,000) legs, myriapods range from having over 750 legs (*Illacme plenipes*) to having fewer than ten legs.

The fossil record of myriapods reaches back into the late Silurian, although molecular evidence suggests a diversification in the Cambrian Period, and Cambrian fossils exist which resemble myriapods.

The scientific study of myriapods is myriapodology.

Anatomy

Myriapods have a single pair of antennae and, in most cases, simple eyes. The mouthparts lie on the underside of the head, with an "epistome" and labrum forming the upper lip, and a pair of maxillae forming the lower lip. A pair of mandibles lie inside the mouth. Myriapods breathe through spiracles that connect to a tracheal system similar to that of insects. There is a long tubular heart that extends through much of the body, but usually few, if any, blood vessels.

Malpighian tubules excrete nitrogenous waste into the digestive system, which typically consists of a simple tube. Although the ventral nerve cord has a ganglion in each segment, the brain is relatively poorly developed.

During mating, male myriapods produce a packet of sperm, or spermatophore, which they must transfer to the female externally; this process is often complex and highly developed. The female lays eggs which hatch as much shortened versions of the adults, with only a few segments and as few as three pairs of legs. The young add additional segments and limbs as they repeatedly moult to reach the adult form.

Ecology

Myriapods are most abundant in moist forests, where they fulfill an important role in breaking down decaying plant material, although a few live in grasslands, semi-arid habitats or even deserts. The majority are detritivorous, with the exception of centipedes, which are chiefly nocturnal predators. Pauropodans and symphylans are small, sometimes microscopic animals that resemble centipedes superficially and live in soils. Millipedes differ from the other groups in having their body segments fused into pairs, giving the appearance that each segment bears two pairs of legs, while the other three groups have a single pair of legs on each body segment.

Although not generally considered dangerous to humans, many myriapods produce noxious secretions (often containing benzoquinones) which can cause temporary blistering and discolouration of the skin.

Classification

There has been much debate as to which arthropod group is most closely related to the Myriapoda. Under the Mandibulata hypothesis, Myriapoda is the sister taxon to Pancrustacea, a group comprising the Crustacea and Hexapoda. Under the Atelocerata hypothesis, Hexapoda is the closest, whereas under the Paradoxopoda hypothesis, Chelicerata is the closest. This last hypothesis, although supported by few, if any, morphological characters, is supported by a number of molecular studies.

There are four classes of extant myriapods, Chilopoda (centipedes), Diplopoda, Pauropoda and Symphyla, containing a total of around 12,000 species. While each of these groups of myriapods is believed to be monophyletic, relationships among them are less certain.

Centipedes

Scolopendra cingulata, a centipede

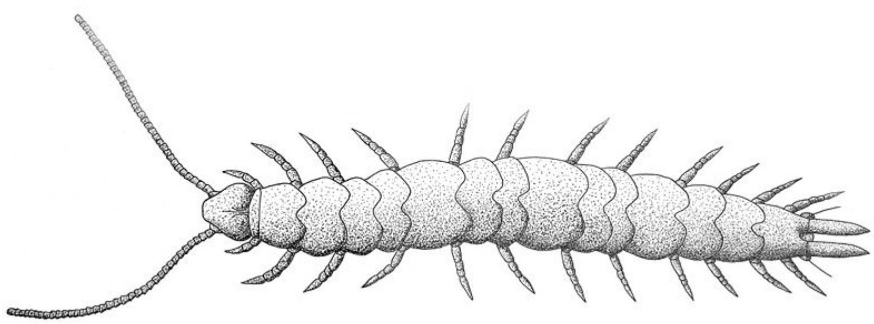
Centipedes make up the order Chilopoda. They are fast, predatory and venomous, hunting mostly at night. There are around 3,300 species, ranging from the diminutive *Nannarup hoffmani* (less than half an inch in length, c. 12 mm) to the giant *Scolopendra gigantea*, which may exceed 30 centimetres (12 in).

Millipedes

Tachypodoiulus niger, a millipede

Most millipedes are slower than centipedes, and feed on leaf litter and detritus. They are distinguished by the fusion of each pair of body segments into a single unit, giving the appearance of having two pairs of legs per segment. Around 8,000 species have been described, which may represent less than a tenth of the true global millipede diversity. One species, *Illacme plenipes* has the greatest number of legs of any animal, with 750. The name "millipede" is a compound word formed from the Latin roots milli ("thousand") and ped ("foot"), although millipedes typically have between 36 and 400 legs. Pill millipedes are much shorter, and are capable of rolling up into a ball, like pillbugs.

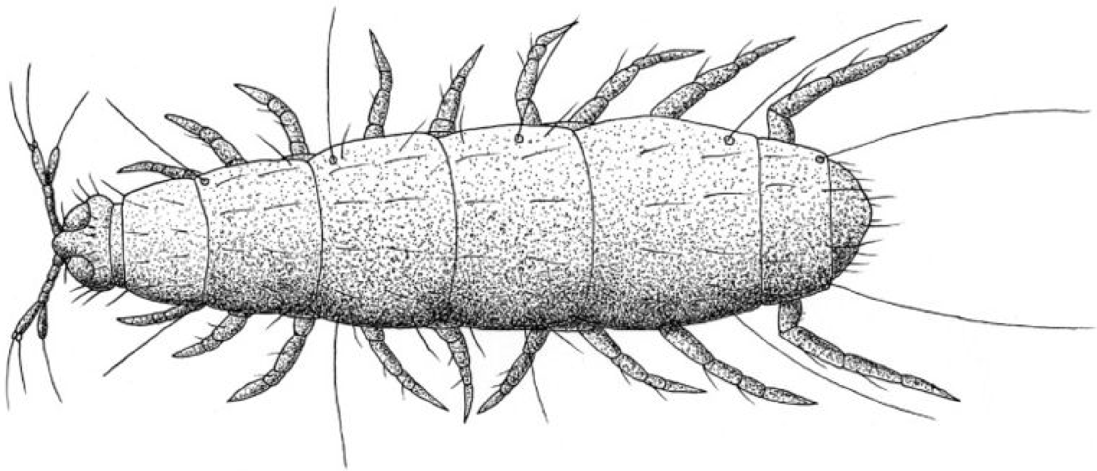
Symphyla



Scutigerella immaculata, a symphylan

About 200 species of symphylans are known worldwide. They resemble centipedes but are smaller and translucent. Many spend their lives as soil infauna, but some live arboreally. Juveniles have six pairs of legs, but, over a lifetime of several years, add an additional pair at each moult so that the adult instar has twelve pairs of legs.

Pauropoda



Pauropus huyxleyi, a pauropodan

Pauropoda is another small group of small myriapods. They are typically 0.5–2.0 mm long and live in the soil on all continents except Antarctica. Over 700 species have been described. They are believed to be the sister group to millipedes, and have the dorsal tergites fused across pairs of segments, similar to the more complete fusion of segments seen in millipedes.

Arthropleuridea

Arthropleurids were ancient myriapods that are now extinct. The most famous members are from the genus *Arthropleura*, which was a giant, probably herbivorous, animal that could be up to 3 metres (9.8 ft) long. Arthropleuridea may be a division of the millipedes.

Hexapoda

Hexapods Temporal range: Early Devonian–Recent	
 A flesh-fly	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	**Hexapoda** Latreille, 1825
Classes & Orders	
Class Insecta (insects) Class Entognatha	

The subphylum **Hexapoda** (from the Greek for *six legs*) constitutes the largest (in terms of number of species) grouping of arthropods and includes the insects as well as three much smaller groups of wingless arthropods: Collembola, Protura, and Diplura (all of these were once considered insects). The Collembola (or springtails) are very abundant in terrestrial environments. *Hexapods* are named for their most distinctive feature: a consolidated thorax with three pairs of legs. Most other arthropods have more than three pairs of legs.

Hexapod morphology

Hexapods have bodies divided into an anterior head, thorax, and posterior abdomen. The head is composed of a presegmental ***acron*** that usually bears eyes (absent in Protura and Diplura), followed by six segments, all closely fused together, with the following appendages:

Segment I. None
Segment II. Antennae (sensory), absent in Protura
Segment III. None
Segment IV. Mandibles (crushing jaws)
Segment V. Maxillae (chewing jaws)

Segment VI. Labium (lower lip)

The mouth lies between the fourth and fifth segments and is covered by a projection from the sixth, called the **labrum** (upper lip). In true insects (class Insecta herein) the mouthparts are exposed or ***ectognathous***, while in other groups they are enveloped or ***endognathous***. Similar appendages are found on the heads of Myriapoda and Crustacea, although these have secondary antennae.

The thorax is composed of three segments, each of which bears a single pair of legs. As is typical of arthropods adapted to life on land, each leg has only a single walking branch composed of five segments, without the gill branches found in some other arthropods. In most insects the second and third thoracic segments also support wings. It has been suggested that these may be homologous to the gill branches of crustaceans, or they may have developed from extensions of the segments themselves.

The abdomen consists of eleven segments in all true insects (often reduced in number in many insect species), but in Protura it has twelve, and in Collembola only six (sometimes reduced to only four). The appendages on the abdomen are extremely reduced, restricted to the external genitalia and sometimes a pair of sensory ***cerci*** on the last segment.

Hexapod relationships

The myriapods have traditionally been considered the closest relatives of the hexapods, based on morphological similarity. These were then considered subclasses of a subphylum called Uniramia or Atelocerata. New work, however, has called this into question, and it appears their closest relatives may be the crustaceans. The non-insect hexapods have variously been considered a single evolutionarily line, typically treated as Class Entognatha (cladogram A), or several lines with different relationships with the Class Insecta. In particular, the Diplura may be more closely related to the Insecta than the Collembola or the Protura (cladogram B). There is also some evidence suggesting that the hexapod groups may not share a common origin, and in particular that the Collembola belong elsewhere.

Molecular analysis suggests that the hexapods diverged from their sister group, the Anostraca (fairy shrimps), at around the start of the Silurian period 440 million years ago - coinciding with the appearance of vascular plants on land.

Chapter 3

Crustacean

Crustacea **Temporal range: 511–0 Ma** **Cambrian to Recent**	
	
Abludomelita obtusata, an amphipod	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	**Crustacea** Brünnich, 1772
Classes & Subclasses	

Thylacocephala?
Branchiopoda

- Phyllopoda
- Sarsostraca

Remipedia
Cephalocarida
Maxillopoda

- Thecostraca
- Tantulocarida
- Branchiura
- Pentastomida

Mystacocarida
Copepoda

Ostracoda

Myodocopa
Podocopa

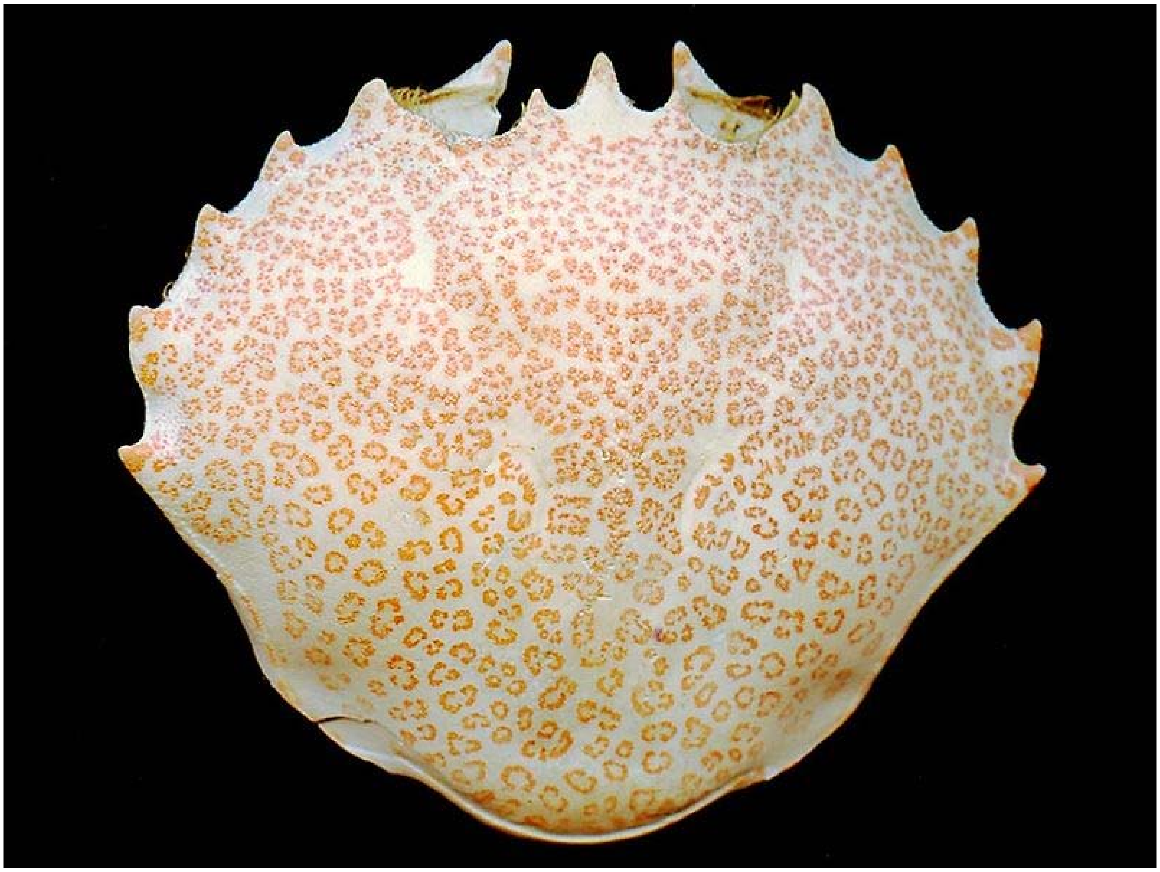
Malacostraca

Phyllocarida
Hoplocarida
Eumalacostraca

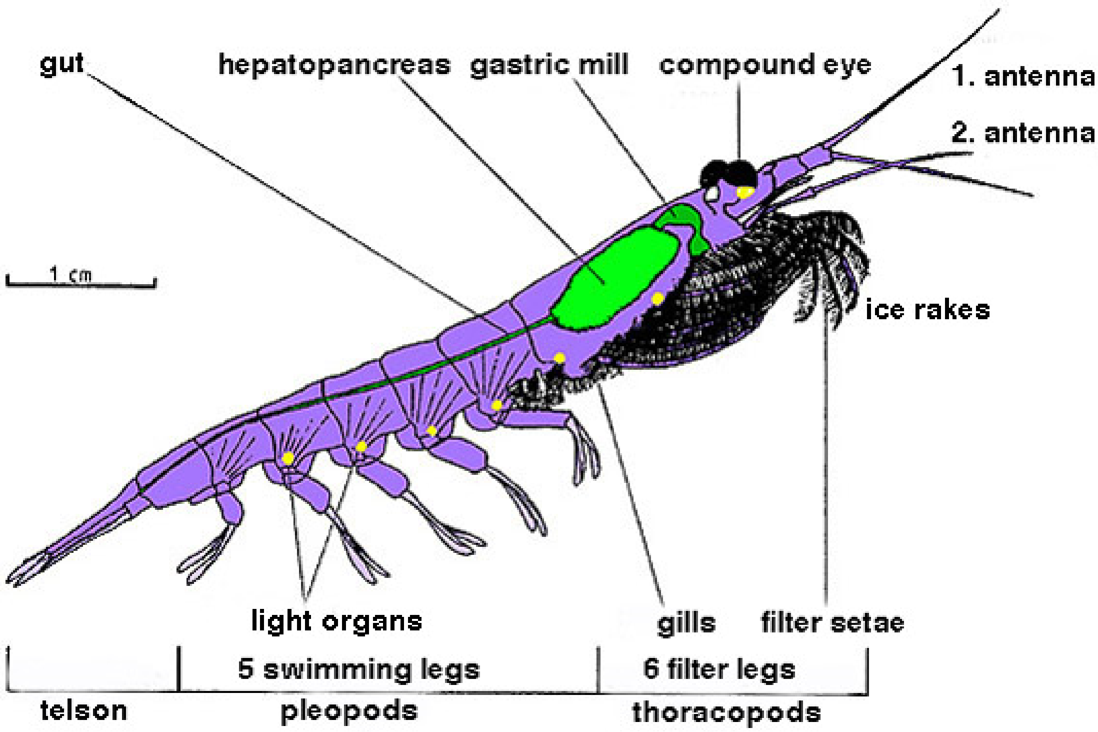
Crustaceans (**Crustacea**) form a very large group of arthropods, usually treated as a subphylum, which includes such familiar animals as crabs, lobsters, crayfish, shrimp, krill and barnacles. The 50,000 described species range in size from *Stygotantulus stocki* at 0.1 mm (0.004 in), to the Japanese spider crab with a leg span of up to 12.5 ft (3.8 m) and a mass of 44 lb (20 kg). Like other arthropods, crustaceans have an exoskeleton, which they moult to grow. They are distinguished from other groups of arthropods, such as insects, myriapods and chelicerates by the possession of biramous (two-parted) limbs, and by the nauplius form of the larvae.

Most crustaceans are free-living aquatic animals, but some are terrestrial (e.g. woodlice), some are parasitic (e.g. fish lice, tongue worms) and some are sessile (e.g. barnacles). The group has an extensive fossil record, reaching back to the Cambrian, and includes living fossils such as *Triops cancriformis*, which has existed apparently unchanged since the Triassic period. More than 10 million tons of crustaceans are produced by fishery or farming for human consumption, the majority of it being shrimps and prawns. Krill and copepods are not as widely fished, but may be the animals with the greatest biomass on the planet, and form a vital part of the food chain. The scientific study of crustaceans is known as carcinology (alternatively, malacostracology, crustaceology or crustalogy), and a scientist who works in carcinology is a carcinologist.

Structure



A shed carapace of a lady crab, part of the hard exoskeleton



Body structure of a typical crustacean - krill

The body of a crustacean is composed of body segments, which are grouped into three regions: the *cephalon* or head, the thorax, and the *pleon* or abdomen. The head and thorax may be fused together to form a cephalothorax, which may be covered by a single large carapace. The crustacean body is protected by the hard exoskeleton, which must be moulted for the animal to grow. The shell around each somite can be divided into a dorsal tergum, ventral sternum and a lateral pleuron. Various parts of the exoskeleton may be fused together.

Each somite, or body segment can bear a pair of appendages: on the segments of the head, these include two pairs of antennae, the mandibles and maxillae; the thoracic segments bear legs, which may be specialised as pereiopods (walking legs) and maxillipeds (feeding legs). The abdomen bears pleopods, and ends in a telson, which bears the anus, and is often flanked by uropods to form a tail fan. The number and variety of appendages in different crustaceans may be partly responsible for the group's success. Crustacean appendages are typically biramous, meaning they are divided into two parts; this includes the second pair of antennae, but not the first, which is uniramous. It is unclear whether the biramous condition is a derived state which evolved in crustaceans, or whether the second branch of the limb has been lost in all other groups. Trilobites, for instance, also possessed biramous appendages.

The main body cavity is an open circulatory system, where blood is pumped into the haemocoel by a heart located near the dorsum. The alimentary canal consists of a straight tube that often has a gizzard-like "gastric mill" for grinding food and a pair of digestive glands that absorb food; this structure goes in a spiral format. Structures that function as kidneys are located near the antennae. A brain exists in the form of ganglia close to the antennae, and a collection of major ganglia is found below the gut.

In many decapods, the first (and sometimes the second) pair of pleopods are specialised in the male for sperm transfer. Many terrestrial crustaceans (such as the Christmas Island red crab) mate seasonally and return to the sea to release the eggs. Others, such as woodlice, lay their eggs on land, albeit in damp conditions. In most decapods, the females retain the eggs until they hatch into free-swimming larvae.

Ecology

The majority of crustaceans are aquatic, living in either marine or fresh water environments, but a few groups have adapted to life on land, such as terrestrial crabs, terrestrial hermit crabs, and woodlice. Marine crustaceans are as ubiquitous in the oceans as insects are on land. The majority of crustaceans are also motile, moving about independently, although a few taxonomic units are parasitic and live attached to their hosts (including sea lice, fish lice, whale lice, tongue worms, and *Cymothoa exigua*, all of which may be referred to as "crustacean lice"), and adult barnacles live a sessile life – they are attached headfirst to the substrate and cannot move independently. Some branchiurans are able to withstand rapid changes of salinity and will also switch hosts from marine to non-marine species. Krill are the bottom layer and the most important part of the food chain in Antarctic animal communities. Some crustaceans are significant invasive species, such as the Chinese mitten crab and the Asian shore crab.

Life cycle

Eggs of *Potamon fluviatile*, a freshwater crab

Zoea larva of the European lobster, *Homarus gammarus*

Mating system

The majority of crustaceans have separate sexes, and reproduce sexually. A small number are hermaphrodites, including barnacles, remipedes, and Cephalocarida. Some may even change sex during the course of their life. Parthenogenesis is also widespread among crustaceans, where viable eggs are produced by a female without needing fertilisation by a male. This occurs in many brachiopods, some ostracods, some isopods, and certain "higher" crustaceans, such as the *Marmorkrebs* crayfish.

Eggs

In many groups of crustaceans, the fertilised eggs are simply released into the water column, while others have developed a number of mechanisms for holding on to the eggs until they are ready to hatch. Most decapods carry the eggs attached to the pleopods, while peracarids, notostracans, anostracans, and many isopods form a brood pouch from the carapace and thoracic limbs. Female Branchiura do not carry eggs in external ovisacs but attach them in rows to rocks and other objects. Most leptostracans and krill carry the eggs between their thoracic limbs; some copepods carry their eggs in special thin-walled sacs, while others have them attached together in long, tangled strings.

Larvae

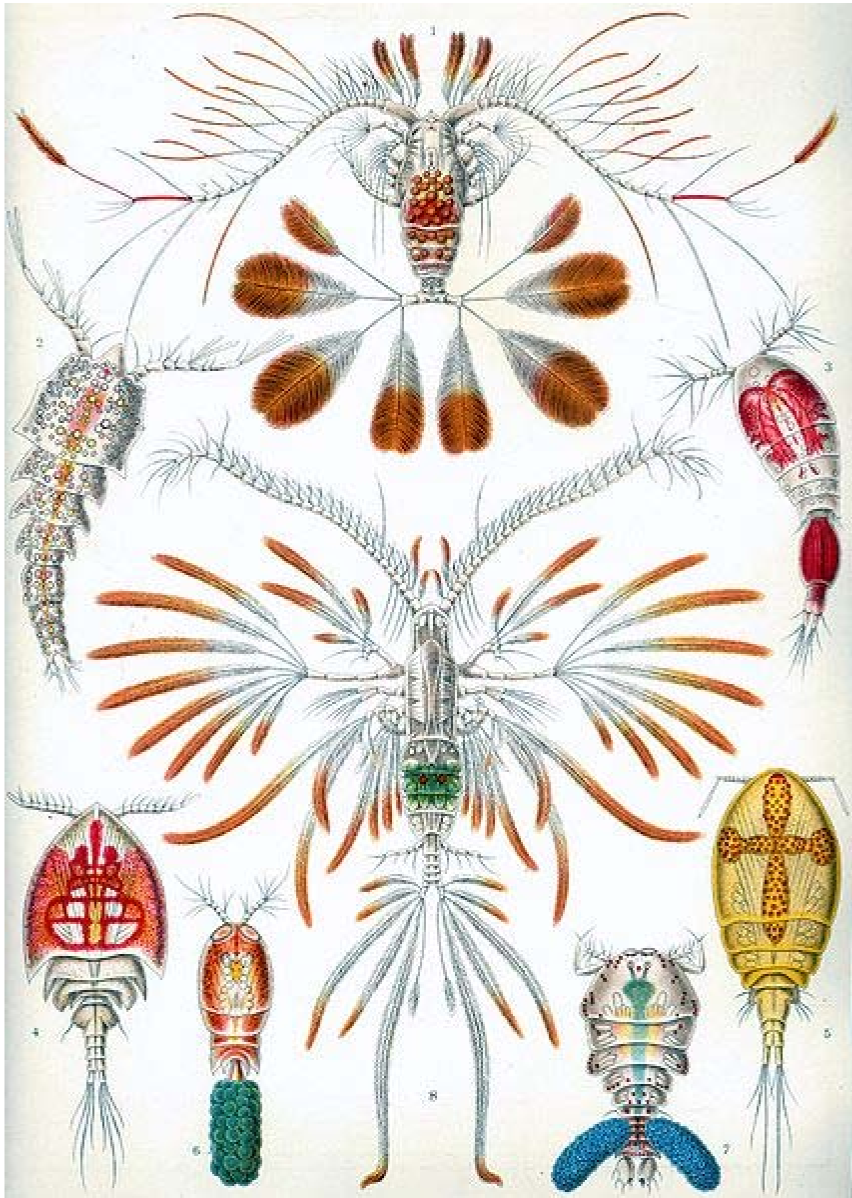
Crustaceans exhibit a number of larval forms, of which the earliest and most characteristic is the nauplius. This has three pairs of appendages, all emerging from the young animal's head, and a single naupliar eye. In most groups, there are further larval stages, including the zoea (pl. zoeæ or zoeas). This name was given to it when naturalists believed it to be a separate species. It follows the nauplius stage and precedes the post-larva. Zoea larvae swim with their thoracic appendages, as opposed to nauplii, which use cephalic appendages, and megalopa, which use abdominal appendages for swimming. It often has spikes on its carapace, which may assist these small organisms in maintaining directional swimming. In many decapods, due to their accelerated development, the zoea is the first larval stage. In some cases, the zoea stage is followed by the mysis stage, and in others, by the megalopa stage, depending on the crustacean group involved.

Classification

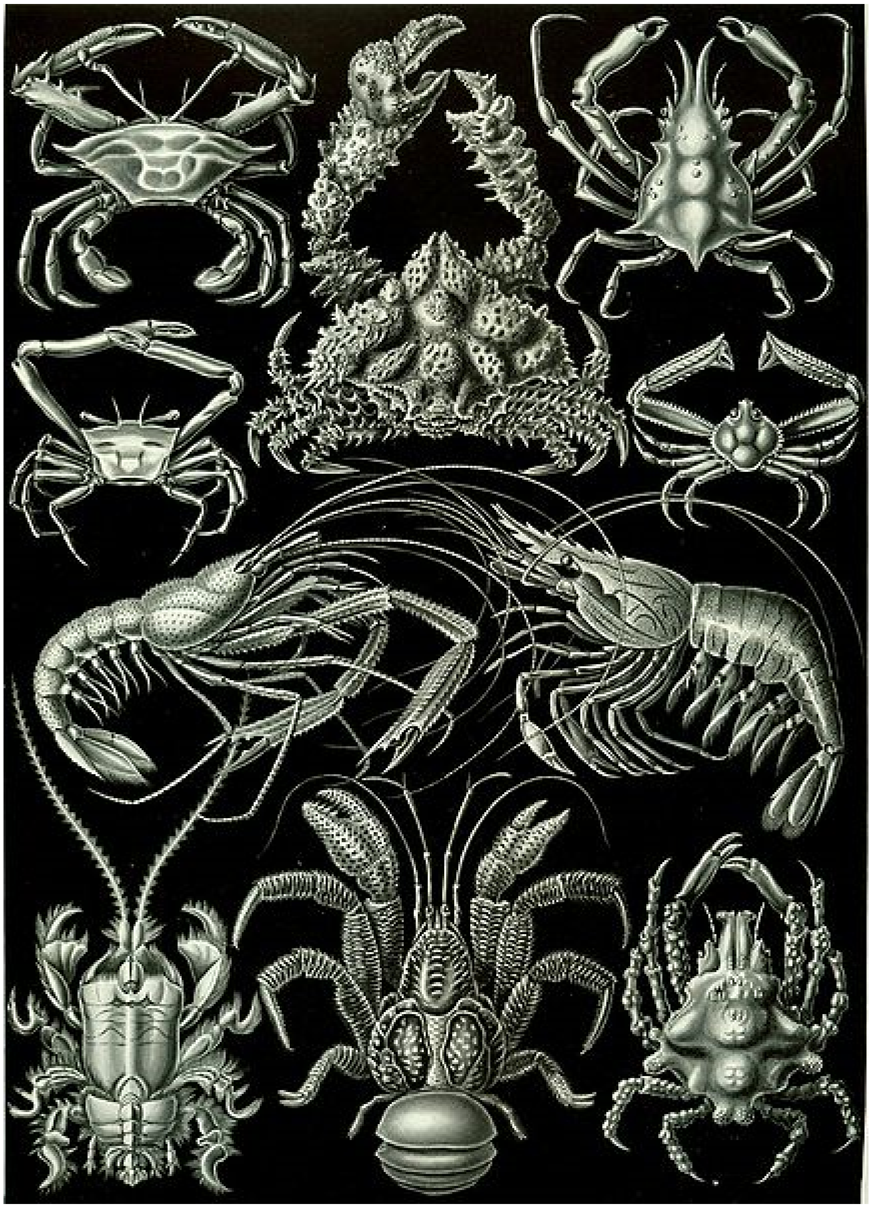
The name "crustacean" dates from the earliest works to describe the animals, including those of Pierre Belon and Guillaume Rondelet, but the name was not used by some later authors, including Carl Linnaeus, who included crustaceans among the "Aptera" in his *Systema Naturae*. The earliest nomenclaturally valid work to use the name "Crustacea" was Morten Thrane Brünnich's *Zoologiæ Fundamenta* in 1772, although he also included chelicerates in the group.

The subphylum Crustacea comprises almost 52,000 described species, although the number of undescribed species may be 10–100 times higher. Although most crustaceans are small, their morphology varies greatly and they include both the largest arthropod in the world – the Japanese spider crab with a leg span of 14 feet (4.3 m) – and the smallest – the 0.1 mm (0.004 in) long *Stygotantulus stocki*. Despite their diversity of form, crustaceans are united by the special larval form known as the nauplius.

The exact relationships of the Crustacea to other taxa are not yet entirely clear. Under the Pancrustacea hypothesis, Crustacea and Hexapoda (insects and allies) are sister groups. Studies using DNA sequences tend to show a paraphyletic Crustacea, with the insects (but not necessarily other hexapods) nested within that clade. Although the classification of crustaceans has been quite variable, the system used by Martin and Davis is the most authoritative, and largely supersedes earlier works. Mystacocarida and Branchiura, here treated as part of Maxillopoda, are sometimes treated as their own classes. Six classes are usually recognised:



Copepods, from Ernst Haeckel's 1904 work *Kunstformen der Natur*



Decapods, from Ernst Haeckel's 1904 work *Kunstformen der Natur*

Class	Members	Orders	Photo
Branchiopoda	brine shrimp Cladocera *Triops*	Anostraca Notostraca Laevicaudata Spinicaudata Cyclestherida Cladocera	 *Daphnia pulex* (Cladocera)
Remipedia		Nectiopoda	
Cephalocarida	horseshoe shrimp	Brachypoda	
Maxillopoda	barnacles copepods	Calanoida Pedunculata Sessilia *c.* 20 others	 *Chthamalus stellatus* (Sessilia)
Ostracoda	ostracods	Myodocopida Halocyprida Platycopida Podocopida	 Cylindroleberididae
Malacostraca	crabs lobsters shrimp krill mantis shrimp woodlice sandhoppers *etc.*	Decapoda Isopoda Amphipoda Stomatopoda *c.* 12 others	 *Gammarus roeseli* (Amphipoda)

Fossil record

Eryma mandelslohi, a fossil decapod from the Jurassic of Bissingen an der Teck, Germany

Crustaceans have a rich and extensive fossil record, which begins with animals such as *Canadaspis* and *Perspicaris* from the Middle Cambrian age Burgess Shale. Most of the major groups of crustaceans appear in the fossil record before the end of the Cambrian, namely the Branchiopoda, Maxillopoda (including barnacles and tongue worms) and Malacostraca; there is some debate as to whether or not Cambrian animals assigned to Ostracoda are truly ostracods, which would otherwise start in the Ordovician. The only classes to appear later are the Cephalocarida, which have no fossil record, and the Remipedia, which were first described from the fossil *Tesnusocaris goldichi*, but do not appear until the Carboniferous. Most of the early crustaceans are rare, but fossil crustaceans become abundant from the Carboniferous onwards.

Norway lobsters on sale at a Spanish market

Within the Malacostraca, no fossils are known for krill, while both Hoplocarida and Phyllopoda contain important groups that are now extinct as well as extant members (Hoplocarida: mantis shrimp are extant, while Aeschronectida are extinct; Phyllopoda: Canadaspidida are extinct, while Leptostraca are extant). Cumacea and Isopoda are both known from the Carboniferous, as are the first true mantis shrimp. In the Decapoda, prawns and polychelids appear in the Triassic, and shrimp and crabs appear in the Jurassic; however, the great radiation of crustaceans occurred in the Cretaceous, particularly in crabs, and may have been driven by the adaptive radiation of their main predators, bony fish. The first true lobsters also appear in the Cretaceous.

Consumption by man

Many crustaceans are consumed by humans, and nearly 10,700,000 tons were produced in 2007; the vast majority of this output is of decapod crustaceans: crabs, lobsters, shrimp, and prawns. Over 60% by weight of all crustaceans caught for consumption are shrimp and prawns, and nearly 80% is produced in Asia, with China alone producing nearly half the world's total. Non-decapod crustaceans are not widely consumed, with only 118,000 tons of krill being caught, despite krill having one of the greatest biomasses on the planet.

Chapter 4

Trilobite

Trilobites Temporal range: Atdabanian – Late Permian	
	
Kainops invius	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	†Trilobitomorpha
Class:	**†Trilobita** Walch, 1771
Orders	

- Agnostida
- Asaphida
- Corynexochida
- Harpetida
- Nectaspida
- Redlichiida
- Lichida
- Phacopida
- Proetida
- Ptychopariida

Trilobites are a well-known fossil group of extinct marine arthropods that form the class **Trilobita**. The first appearance of trilobites in the fossil record defines the base of the Atdabanian stage of the Early Cambrian period (526 million years ago), and they flourished throughout the lower Paleozoic era before beginning a drawn-out decline to extinction when, during the Devonian, all trilobite orders, with the sole exception of Proetida, died out. Trilobites finally disappeared in the mass extinction at the end of the Permian about 250 million years ago. The trilobites were the most successful species roaming the earth for over 270 million years.

When trilobites first appeared in the fossil record they were already highly diverse and geographically dispersed. Because trilobites had wide diversity and an easily fossilized exoskeleton an extensive fossil record was left, with some 17,000 known species spanning Paleozoic time. The study of these fossils has facilitated important contributions to biostratigraphy, paleontology, evolutionary biology and plate tectonics. Trilobites are often placed within the arthropod subphylum Schizoramia within the superclass Arachnomorpha (equivalent to the Arachnata), although several alternative taxonomies are found in the literature.

Trilobites had many life styles; some moved over the sea-bed as predators, scavengers or filter feeders and some swam, feeding on plankton. Most life styles expected of modern marine arthropods are seen in trilobites, with the possible exception of parasitism (where there is still scientific debate). Some trilobites (particularly the family Olenidae) are even thought to have evolved a symbiotic relationship with sulfur-eating bacteria from which they derived food.

Phylogeny

Redlichida, such as this *Paradoxides*, may represent the ancestral trilobites.

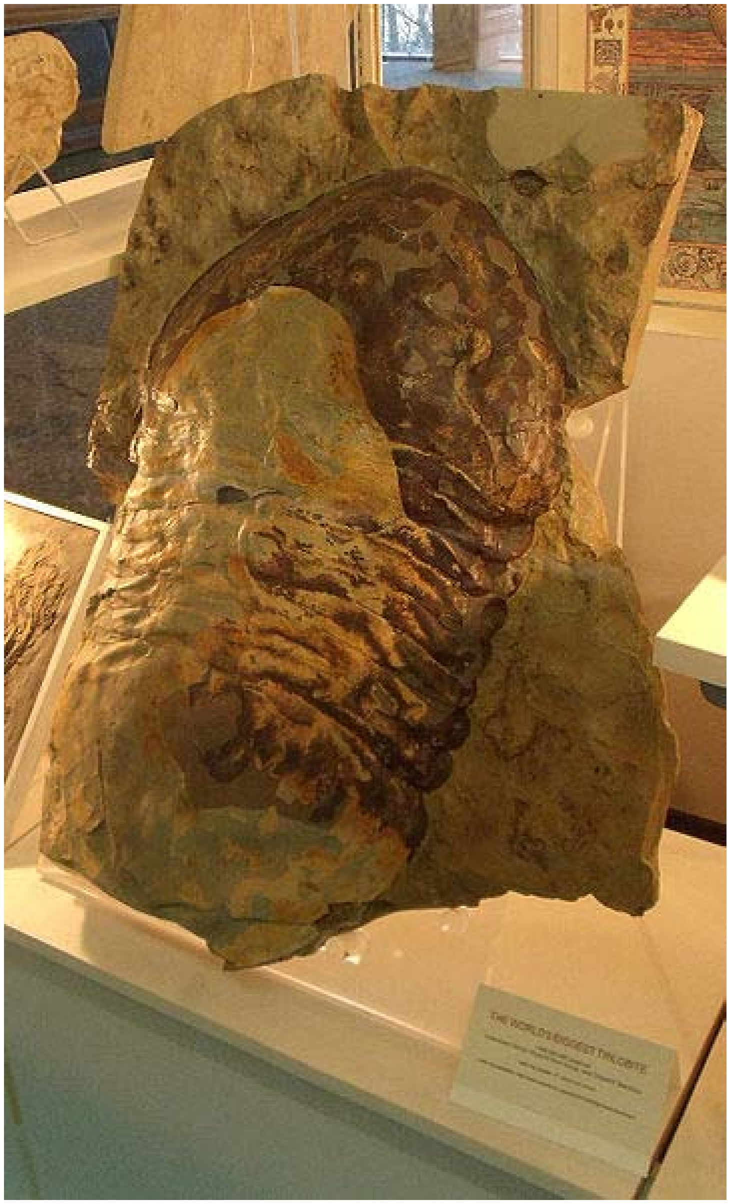
Despite their rich fossil record with thousands of genera found throughout the world, the taxonomy and phylogeny of trilobites have many uncertainties. The systematic division of trilobites into nine distinct orders is represented by a widely held view that will inevitably change as new data emerges. Except possibly for the members of order Phacopida, all trilobite orders appeared prior to the end of the Cambrian. Most scientists believe that order Redlichiida, and more specifically its suborder Redlichiina, contains a common ancestor of all other orders, with the possible exception of the Agnostina. While many potential phylogenies are found in the literature, most have suborder Redlichiina giving rise to orders Corynexochida and Ptychopariida during the Lower Cambrian, and the Lichida descending from either the Redlichiida or Corynexochida in the Middle Cambrian. Order Ptychopariida is the most problematic order for trilobite classification. In the 1959 Treatise on Invertebrate Paleontology, what are now members of orders Ptychopariida, Asaphida, Proetida, and Harpetida were grouped together as order Ptychopariida; subclass Librostoma was erected in 1990 to encompass all of these orders, based on their shared ancestral character of a natant (unattached) hypostome. The most recently recognized of the nine trilobite orders, Harpetida, was erected in 2002. The progenitor of order Phacopida is unclear.

Relationship to other taxa

Once soft-part anatomy had been recovered, the trilobites were originally allied to the Crustacea; however, this suggestion has since fallen out of favour. A relationship with the Chelicerata, in a clade termed Arachnomorpha (Arachnata), was in vogue for some time; a position in the Mandibulata (=Myriapoda + Crustacea + Hexapoda) stem-group may be a more parsimonious alternative.

Physical description

Triarthrus Eatoni - ventral side



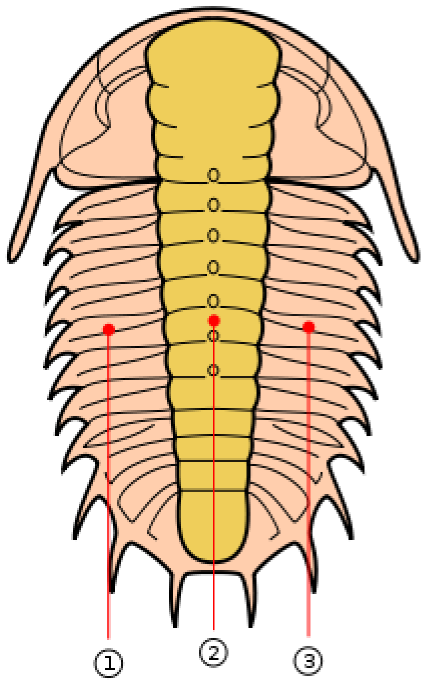
Cast of *Isotelus rex*, the largest known trilobite.

When trilobites are found, only the exoskeleton is preserved (often in an incomplete state) in all but a handful of locations. A few locations (*Lagerstätten*) preserve identifiable soft body parts (legs, gills, musculature & digestive tract) and enigmatic traces of other structures (e.g. fine details of eye structure) as well as the exoskeleton.

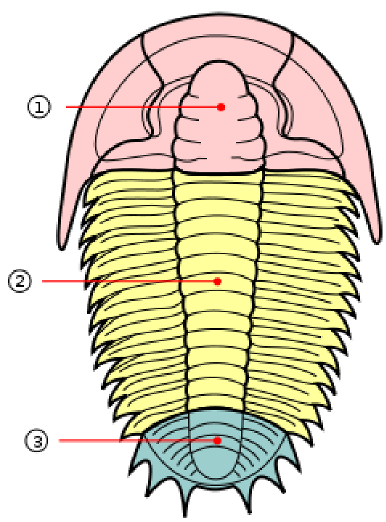
Trilobites range in length from 1 millimetre (0.04 in) to 72 centimetres (28 in), with a typical size range of 3–10 cm (1.2–3.9 in). The world's largest trilobite, *Isotelus rex*, was found in 1998 by Canadian scientists in Ordovician rocks on the shores of Hudson Bay.

Exoskeleton

Trilobite external morphology



Trilobites are so named for the three longitudinal lobes: 1 – left pleural lobe; 2 – axial lobe; 3 – right pleural lobe



The trilobite body is divided into three major sections (tagmata): 1 – cephalon; 2 – thorax; 3 – pygidium

The exoskeleton is composed of calcite and calcium phosphate minerals in a protein lattice of chitin that covers the upper surface (dorsal) of the trilobite and curled round the lower edge to produce a small fringe called the "doublure". Three distinctive *tagmata* (sections) are present: cephalon (head); thorax (body) and pygidium (tail).

Terminology

As might be expected for a group of animals comprising c. 5,000 genera, the morphology and description of trilobites can be complex. However, despite morphological complexity and an unclear position within higher classifications, there are a number of characters that distinguish the trilobites from other arthropods: a generally sub-elliptical, dorsal, chitinous exoskeleton divided longitudinally into three distinct lobes (from which the group gets its name); having a distinct, relatively large head shield (cephalon) articulating axially with a thorax comprising articulated transverse segments, the hindmost of which are almost invariably fused to form a tail shield (pygidium). When describing differences between trilobite taxa, the presence, size, and shape of the cephalic features are often mentioned.

During moulting, the exoskeleton generally split between the head and thorax, which is why so many trilobite fossils are missing one or the other. In most groups facial sutures on the cephalon helped facilitate moulting. Similar to lobsters and crabs, trilobites would have physically "grown" between the moult stage and the hardening of the new exoskeleton.

Cephalon

Thorax

An enrolled phacopid trilobite *Phacops rana crassituberculata*

The thorax is a series of articulated segments that lie between the cephalon and pygidium. The number of segments varies between 2 and 61 with most species in the 2 to 16 range.

Each segment consists of the central axial ring and the outer plurae which protected the limbs and gills. The plurae are sometimes abbreviated to save weight or extended to form long spines. Apodemes are bulbous projections on the ventral surface of the exoskeleton to which most leg muscles attached, although some leg muscles attached directly to the exoskeleton. Distinguishing where the thorax ends and the pygidium begins can be problematic and many segment counts suffer from this problem.

Trilobite fossils are often found "enrolled" (curled up) like modern pill-bugs for protection; evidence suggests enrollment helped protect against the inherent weakness of the arthropod cuticle that was exploited by anomalocarid predators.

Some trilobites achieved a fully closed capsule (e.g. *Phacops*), while others with long pleural spines (e.g. *Selenopeltis*) left a gap at the sides or those with a small pygidium (e.g. *Paradoxides*) left a gap between the cephalon and pygidium. In *Phacops*, the pleurae overlap a smooth bevel (facet) allowing a close seal with the doublure. The doublure carries a panderian notch or protuberance on each segment to prevent over rotation and achieve a good seal. Even in an agnostid, with only 2 articulating thoracic segments, the process of enrollment required a complex musculature to contract the exoskeleton and return to the flat condition.

Pygidium

The pygidium is formed from a number of segments and the telson fused together. Segments in the pygidium are similar to the thoracic segments (bearing biramous limbs) but are not articulated. Trilobites can be described based on the pydigium being micropygous (pydigium smaller than cephalon), isopygous (pydigium equal in size to cephalon), or macropygous (pydigium larger than cephalon).

Prosopon (surface sculpture)

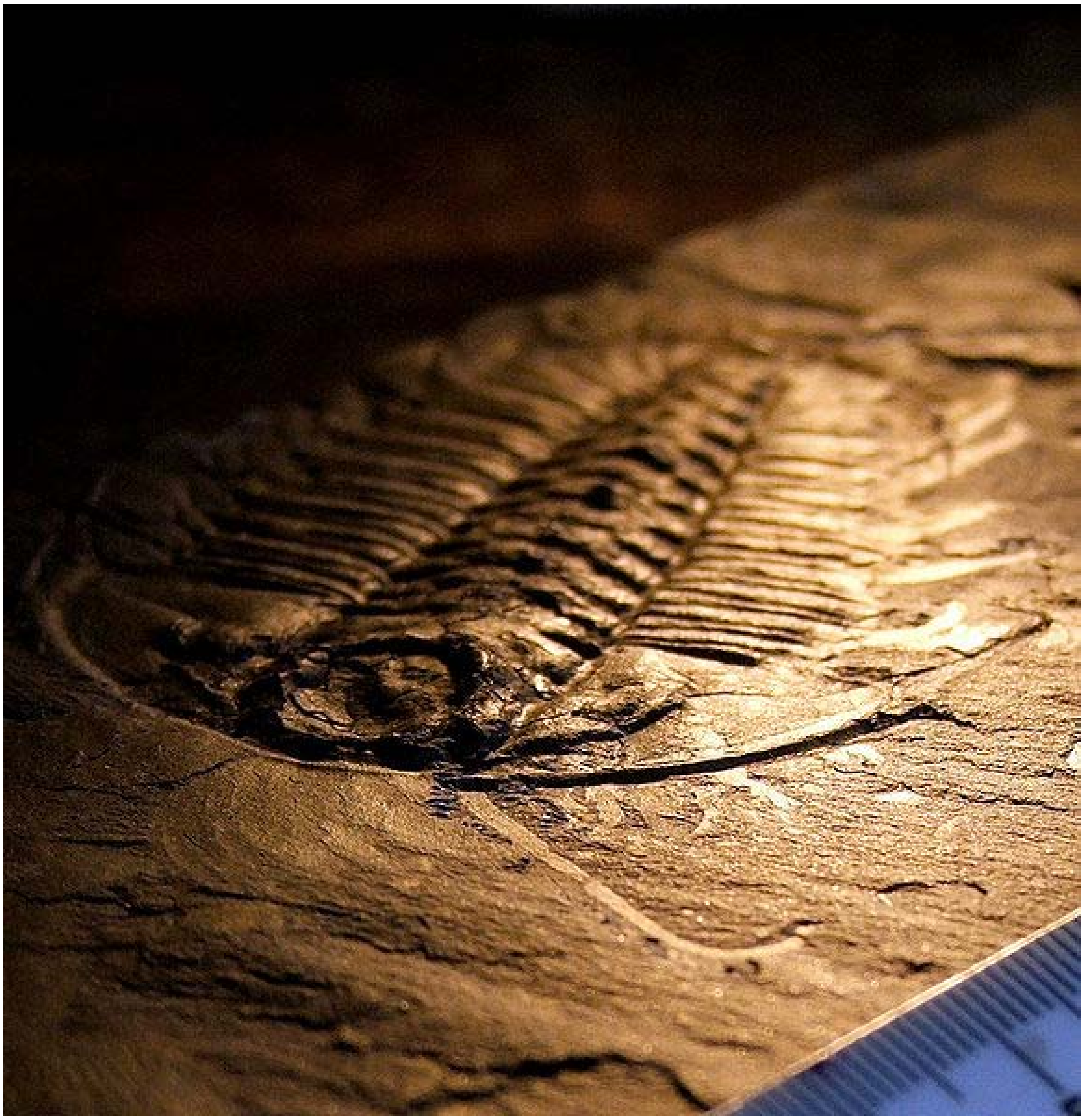
Trilobite exoskeletons show a variety of small-scale structures collectively called prosopon. Prosopon does not include large scale extensions of the cuticle (e.g. hollow pleural spines) but to finer scale features, such as ribbing, domes, pustules, pitting, ridging and perforations. The exact purpose of the prosopon is not resolved but suggestions include structural strengthening, sensory pits or hairs, preventing predator attacks and maintaining aeration while enrolled. In one example, alimentary ridge networks (easily visible in Cambrian trilobites) might have been either digestive or respiratory tubes in the cephalon and other regions.

Spines

Koneprusia brutoni, an example of a species with elaborate spines from the Devonian Hamar Laghdad Formation, Alnif, Morocco

Some trilobites such as those of the order Lichida evolved elaborate spiny forms, from the Ordovician until the end of the Devonian period. Examples of these specimens have been found in the Hamar Laghdad Formation of Alnif in Morocco. There is, however, a serious counterfeiting and fakery problem with much of the Moroccan material that is offered commercially. Spectacular spined trilobites have also been found in western Russia; Oklahoma, USA; and Ontario, Canada.

Some trilobites had horns on their heads similar to those of modern beetles. Based on the size, location, and shape of the horns the most likely use of the horns was combat for mates, making the Asaphida family Raphiophoridae the earliest exemplars of this behavior. A conclusion likely to be applicable to other trilobites as well, such as in the Phacopid trilobite genus *Walliserops* that developed spectacular tridents.



An exceptionally well preserved trilobite from the Burgess Shale. The antennæ and legs are preserved as reflective carbon films.

Soft body parts

Only 21 or so species are described from which soft body parts are preserved, so some features (e.g. the posterior antenniform cerci preserved only in *Olenoides serratus*) remain difficult to assess in the wider picture.

Appendages

Trilobites had a single pair of preoral antennae and otherwise undifferentiated biramous limbs (2, 3 or 4 cephalic pairs, followed by a variable number of thorax + pygidium pairs). Each exopodite (walking leg) had 6 or 7 segments, homologous to other early arthropods. Expodites are attached to the coxa which also bore a feather-like epipodite, or gill branch, which was used for respiration and, in some species, swimming. The base of the coxa, the gnathobase, sometimes have heavy, spiny adaptations which were used to tear at the tissues of prey. The last exopodite segment usually had claws or spines. Many examples of hairs on the legs suggest adaptations for feeding (as for the gnathobases) or sensory organs to help with walking.

Digestive tract

The toothless mouth of trilobites was situated on the rear edge of the hypostome (facing backwards), in front of the legs attached to the cephalon. The mouth is linked by a small esophagus to the stomach that lay forward of the mouth, below the glabella. The "intestine" led backwards from there to the pygidium. The "feeding limbs" attached to the cephalon are thought to have fed food into the mouth, possibly "slicing" the food on the hypostome and/or gnathobases first. Alternative lifestyles are suggested, with the cephalic legs used to disturb the sediment to make food available. A large glabella, (implying a large stomach), coupled with an impendent hypostome has been used as evidence of more complex food sources, i.e. possibly a carnivorous lifestyle.

Internal organs

While there is direct and implied evidence for the presence and location of the mouth, stomach and digestive tract (see above) the presence of heart, brain and liver are only implied (although "present" in many reconstructions) with little direct geological evidence.

Musculature

Although rarely preserved, long lateral muscles extended from the cephalon to mid way down the pygidium, attaching to the axial rings allowing enrollment while separate muscles on the legs tucked them out of the way.

Sensory organs

Many trilobites had complex eyes; they also had a pair of antennae. Some trilobites were blind, probably living too deep in the sea for light to reach them. As such, they became secondarily blind in this branch of trilobite evolution. Other trilobites (e.g. *Phacops rana* and *Erbenochile erbeni*) had large eyes that were for use in more well lit, predator-filled waters.

Antennae

The pair of antennae suspected in most trilobites (and preserved in a few examples) were highly flexible to allow them to be retracted when the trilobite was enrolled. Also, one species (*Olenoides serratus*) preserves antennae-like *cerci* that project from the rear of the trilobite.

Eyes

Even the earliest trilobites had complex, compound eyes with lenses made of calcite (a characteristic of all trilobite eyes), confirming that the eyes of arthropods and probably other animals could have developed before the Cambrian. Improving eyesight of both predator and prey in marine environments has been suggested as one of the evolutionary pressures furthering an apparent rapid development of new life forms during what is known as the Cambrian Explosion.

Trilobite eyes were typically compound, with each lens being an elongated prism. The number of lenses in such an eye varied: some trilobites had only one, while some had thousands of lenses in a single eye. In compound eyes, the lenses were typically arranged hexagonally. The fossil record of trilobite eyes is complete enough that their evolution can be studied through time, which compensates to some extent the lack of preservation of soft internal parts.

Lenses of trilobites' eyes were made of calcite (calcium carbonate, $CaCO_3$). Pure forms of calcite are transparent, and some trilobites used crystallographically oriented, clear calcite crystals to form each lens of each of their eyes. Rigid calcite lenses would have been unable to accommodate to a change of focus like the soft lens in a human eye would; however, in some trilobites the calcite formed an internal doublet structure, giving superb depth of field and minimal spherical aberration, as discovered by French scientist René Descartes and Dutch physicist Christiaan Huygens in the 17th century. A living species with similar lenses is the brittle star *Ophiocoma wendtii*.

In other trilobites, with a Huygens interface apparently missing, a gradient index lens is invoked with the refractive index of the lens changing towards the center.

- Holochroal eyes had a great number (sometimes over 15,000) of small (30–100 µm, rarely larger) lenses. Lenses were hexagonally close packed, touching each other, with a single corneal membrane covering all lenses. Holochroal eyes had no sclera, the white layer covering the eyes of most modern arthropods. Holochroal eyes are the ancestral eye of trilobites, and are by far the most common, found in all orders and through the entirety of the Trilobites' existence. Little is known of the early history of holochroal eyes; Lower and Middle Cambrian trilobites rarely preserve the visual surface.

The schizochroal eye of *Erbenochile erbenii*; the eye shade is unequivocal evidence that some trilobites were diurnal.

- Schizochroal eyes typically had fewer (to around 700), larger lenses than holochroal eyes and are found only in Phacopida. Lenses were separate, with each lens having an individual cornea which extended into a rather large sclera. Schizochroal eyes appear quite suddenly in the early Ordovician, and were presumably derived from a holochroal ancestor. Field of view (all around vision), eye placement and coincidental development of more efficient enrollment mechanisms point to the eye as a more defensive "early warning" system than directly aiding in the hunt for food. Modern eyes which are functionally equivalent to the schizochroal eye were not thought to exist, but are found in the modern insect species *Xenos peckii*.

- Abathochroal eyes are found only in Cambrian Eodiscina, had around 70 small separate lenses that had individual cornea. The sclera was separate from the cornea, and did not run as deep as the sclera in schizochroal eyes. Although well preserved examples are sparse in the early fossil record, abathochroal eyes have been recorded in the lower Cambrian, making them among the oldest known. Environmental conditions seem to have resulted in the later loss of visual organs in many Eodiscina.

Secondary blindness is not uncommon, particularly in long lived groups such as the Agnostida and Trinucleioidea. In Proetida and Phacopina from western Europe and particularly Tropidocoryphinae from France (where there is good stratigraphic control), there are well studied trends showing progressive eye reduction between closely related species that eventually leads to blindness.

Several other structures on trilobites have been explained as photo-receptors. Of particular interest are "macula", the small areas of thinned cuticle on the underside of the hypostome. In some trilobites macula are suggested to function as simple "ventral eyes" that could have detected night and day or allowed a trilobite to navigate while swimming (or turned) upside down.

Sensory pits

There are several types of prosopon that have been suggested as sensory apparatus collecting chemical or vibrational signals. The connection between large pitted fringes on the cephalon of Harpetida and Trinucleoidea with corresponding small or absent eyes makes for an interesting possibility of the fringe as a "compound ear".

Development

Trilobites grew through successive moult stages called instars, in which existing segments increased in size and new trunk segments appeared at a sub-terminal generative zone during the anamorphic phase of development. This was followed by the epimorphic developmental phase, in which the animal continued to grow and moult, but no new trunk segments were expressed in the exoskeleton. The combination of anamorphic and epimorphic growth constitutes the hemianamorphic developmental mode that is common among many living arthropods.

Trilobite development was unusual in the way in which articulations developed between segments, and changes in the development of articulation gave rise to the conventionally recognized developmental phases of the trilobite life cycle (divided into 3 stages), which are not readily compared with those of other arthropods. Actual growth and change in external form of the trilobite would have occurred when the trilobite was soft shelled, following moulting and before the next exoskeleton hardened.

Trilobite larvae are known from the Cambrian to the Carboniferous and from all sub-orders. As instars from closely related taxa are more similar than instars from distantly related taxa, trilobite larvae provide morphological information important in evaluating high-level phylogenetic relationships among trilobites.

By comparison with living arthropods, trilobites are thought to have reproduced sexually, producing eggs, albeit without undoubted examples in the fossil record. Some species may have kept eggs or larvae in a brood pouch forward of the glabella, particularly when the ecological niche was challenging to larvae. Size and morphology of the first calcified stage are highly variable between (but not within) trilobite taxa, suggesting some trilobites passed through more growth within the egg than others. Early developmental stages prior to calcification of the exoskeleton are a possibility (suggested for fallotaspids), but so is calcification and hatching coinciding.

The earliest post-embryonic trilobite growth stage known with certainty are the "protaspid" stages (anamorphic phase). Starting with an indistinguishable proto-cephalon and proto-pygidium (anaprotaspid) a number of changes occur ending with a transverse furrow separating the proto-cephalon and proto-pygidium (metaprotaspid) that can continue to add segments. Segments are added at the posterior part of the pygidium but, all segments remain fused together.

The "meraspid" stages (anamorphic phase) are marked by the appearance of an articulation between the head and the fused trunk. Prior to the onset of the first meraspid stage the animal had a two-part structure — the head and the plate of fused trunk segments, the pygidium. During the meraspid stages, new segments appeared near the rear of the pygidium as well as additional articulations developing at the front of the pygidium, releasing freely articulating segments into the thorax. Segments are generally added one per moult (although two per moult and one every alternate moult are also recorded), with number of stages equal to the number of thoracic segments. A substantial amount of growth, from less than 25% up to 30%–40%, probably took place in the meraspid stages.

The "holaspid" stages (epimorphic phase) commence when a stable, mature number of segments has been released into the thorax. Moulting continued during the holaspid stages, with no changes in thoracic segment number. Some trilobites are suggested to have continued moulting and growing throughout the life of the individual, albeit at a slower rate on reaching maturity.

Some trilobites showed a marked transition in morphology at one particular instar, which has been called "trilobite metamorphosis". Radical change in morphology is linked to the loss or gain of distinctive features that mark a change in mode of life. A change in lifestyle during development has significance in terms of evolutionary pressure, as the trilobite could pass through several ecological niches on the way to adult development and changes would strongly affect survivor-ship and dispersal of trilobite taxa. It is worth noting that trilobites with all protaspid stages solely planktonic and later meraspid stages benthic (e.g. asaphids) failed to last through the Ordovician extinctions, while trilobites that were planktonic for only the first protaspid stage before metamorphosing into benthic forms survived (e.g. lichids, phacopids). Pelagic larval life-style proved ill-adapted to the rapid onset of global climatic cooling and loss of tropical shelf habitats during the Ordovician.

Fossil record

Walliserops trifurcatus, from Djebel Oufaten, Morocco

The earliest trilobites known from the fossil record are fallotaspids (order Redlichiida, suborder Olenellina, superfamily Fallotaspidoidea) and bigotinids (order Ptychopariida, superfamily Ellipsocephaloidea) dated to some 540 to 520 million years ago. Contenders for the earliest trilobites include *Profallotaspis jakutensis* (Siberia), *Fritzaspis sp.* (western USA), *Hupetina antiqua* (Morocco) and *Serrania gordaensis* (Spain). All trilobites are thought to have originated in present day Siberia, with subsequent distribution and radiation from this location.

Fallotaspids lack facial sutures, that is to say fallotaspids are thought to pre-date facial sutures (as opposed to a group that secondarily lost facial sutures). Fallotaspids are strongly suggested to be the ancestral trilobite stock: absence of facial sutures; apparently un-calcified protaspid stages and fallotaspids underlying (pre-dating) or co-existing with all other trilobite occurrences. However, recent developments suggest the picture is more complicated, and likely to change as more information comes to light.

Origins

Early trilobites show all of the features of the trilobite group as a whole; there do not seem to be any transitional or ancestral forms showing or combining the features of trilobites with other groups (e.g. early arthropods). Morphological similarities between trilobites and early arthropod-like creatures such as *Spriggina*, *Parvancorina*, and other "trilobitomorphs" of the Ediacaran period of the Precambrian are ambiguous enough to make detailed analysis of their ancestry far from compelling. Morphological similarities between early trilobites and other Cambrian arthropods (e.g. the Burgess Shale fauna and the Maotianshan shales fauna) make analysis of ancestral relationships difficult. However, it is still reasonable to assume that the trilobites share a common ancestor with other arthropods prior to the Ediacaran-Cambrian boundary. Evidence suggests significant diversification had already occurred prior to the preservation of trilobites in the fossil record, easily allowing for the "sudden" appearance of diverse trilobite groups with complex, derived characteristics (e.g. eyes).

Radiation and extinction

For such a long lasting group of animals, it is no surprise that trilobite evolutionary history is marked by a number of extinction events where unsuccessful groups perished while surviving groups diversified to fill ecological niches with more successful adaptations. Generally, trilobites maintained high diversity levels throughout the Cambrian and Ordovician periods before entering a drawn out decline in the Devonian culminating in final extinction of the last few survivors at the end of the Permian period.

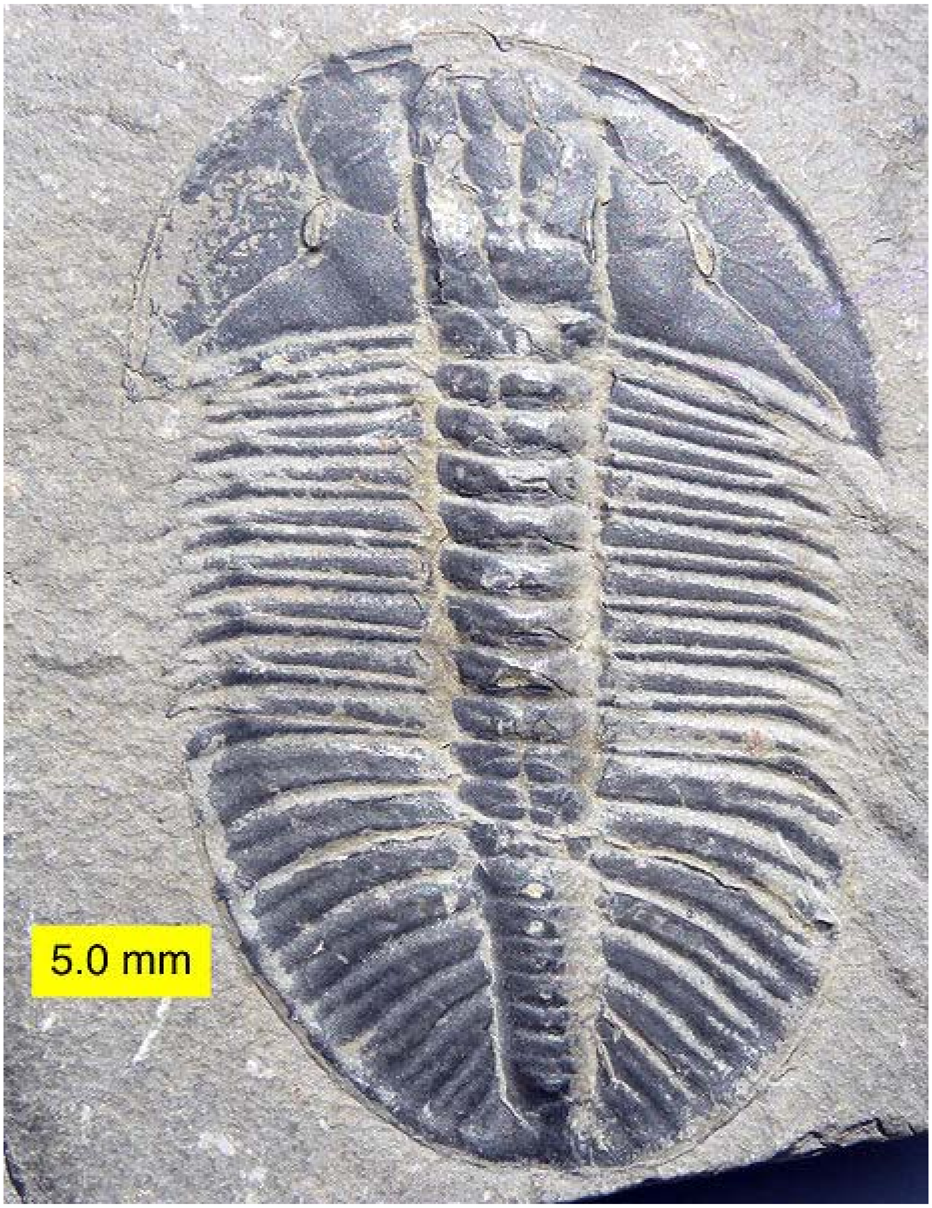
Evolutionary trends

Principal evolutionary trends from primitive morphologies (e.g. eoredlichids) include the origin of new types of eyes, improvement of enrollment and articulation mechanisms, increased size of pygidium (micropygy to isopygy) and development of extreme spinosity in certain groups. Changes also included narrowing of the thorax and increasing or decreasing numbers of thoracic segments. Specific changes to the cephalon are also noted; variable glabella size and shape, position of eyes and facial sutures & hypostome specialization. Several morphologies appeared independently within different major taxa (e.g. eye reduction or miniaturization).

Pre-Cambrian

Phylogenetic biogeographic analysis of Early Cambrian Olenellidae and Redlichidae suggests that a uniform trilobite fauna existed over Laurentia, Gondwana and Siberia before the tectonic breakup of the super-continent Pannotia between 600 million years ago and 550 million years ago. Tectonic break up of Pannotia then allowed for the diversification and radiation expressed later in the Cambrian as the distinctive olenellid province (Laurentia, Siberia and Baltica) and the separate Redlichid province (Australia, Antarctica and China). Break up of Pannotia significantly pre-dates the first appearance of trilobites in the fossil record, supporting a long and cryptic development of trilobites extending perhaps as far back as 700 million years ago or possibly further.

Cambrian



Olenoides erratus from the Mt. Stephen Trilobite Beds (Middle Cambrian) near Field, British Columbia, Canada

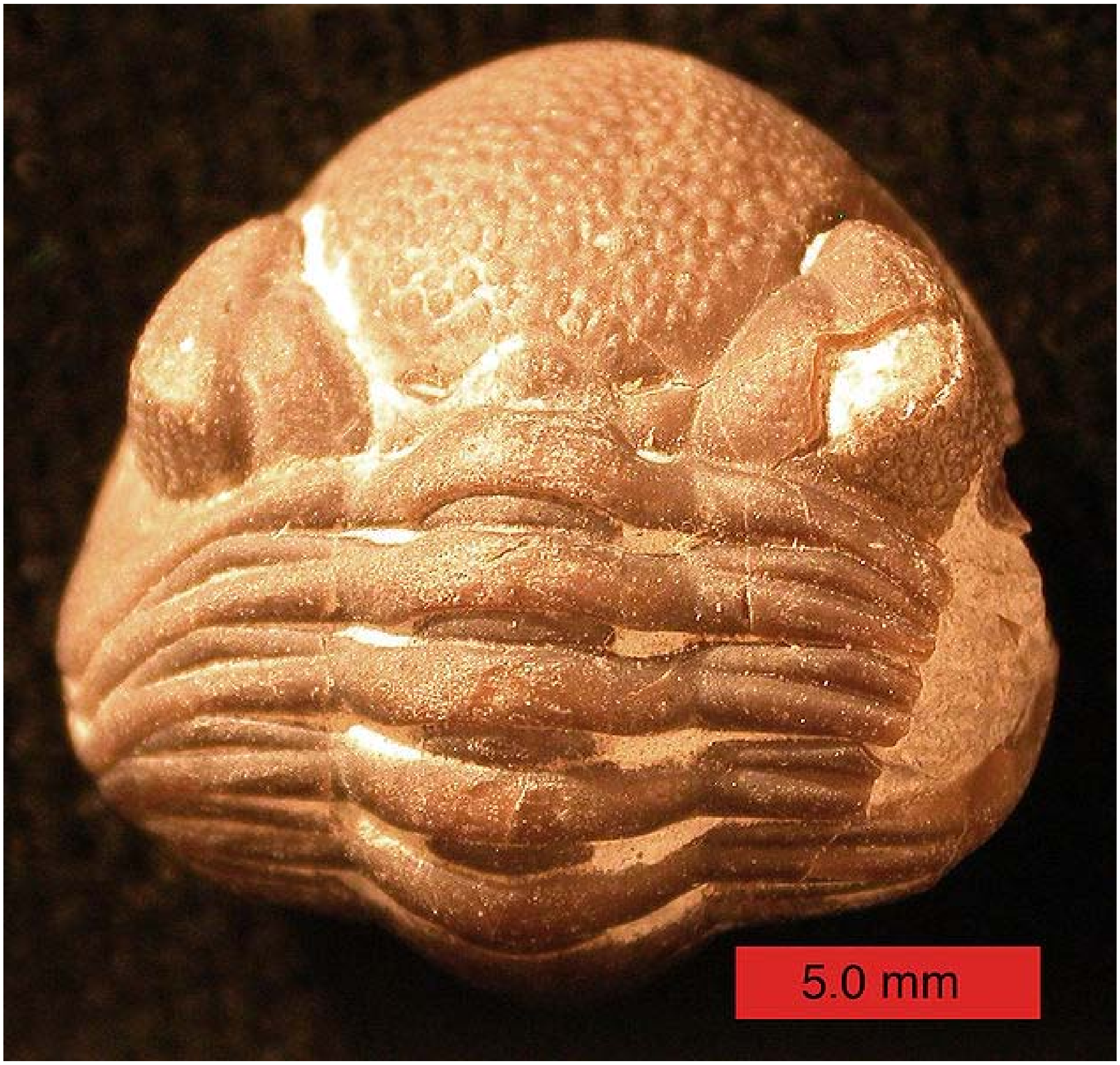
Very shortly after trilobite fossils appeared in the lower Cambrian, they rapidly diversified into the major orders that typified the Cambrian - Redlichiida, Ptychopariida, Agnostida and Corynexochida. The first major crisis in the trilobite fossil record occurred in the Middle Cambrian, surviving orders developed isopygus or macropygius bodies and developed thicker cuticles, allowing better defense against predators. The end Cambrian mass extinction event marked a major change in trilobite fauna; almost all Redlichiida (including the Olenelloidea) and most Late Cambrian stocks went extinct. A continuing decrease in Laurentian continental shelf area is recorded at the same time as the extinctions, suggesting major environmental upheaval.

Ordovician

Cheirurus sp., middle Ordovician age, Volkhov River, Russia

The Early Ordovician is marked by vigorous radiations of articulate brachiopods, bryozoans, bivalves, echinoderms, and graptoloids with many groups appearing in the fossil record for the first time. Although intra-species trilobite diversity seems to have peaked during the Cambrian, trilobites were still active participants in the Ordovician radiation event with a new fauna taking over from the old Cambrian one. Phacopida and Trinucleioidea are characteristic forms, highly differentiated and diverse, most with uncertain ancestors. The Phacopida and other "new" clades almost certainly had Cambrian forebears, but the fact that they have avoided detection is a strong indication that novel morphologies were developing very rapidly. Changes within the trilobite fauna during the Ordovician foreshadowed the mass extinction at the end of the Ordovician allowing many families to continue into the Silurian with little disturbance. Ordovician trilobites were successful at exploiting new environments, notably reefs. However, the end Ordovician mass extinction did not leave the trilobites unscathed; some distinctive and previously successful forms such as the Trinucleioidea and Agnostida became extinct. The Ordovician marks the last great diversification period amongst the trilobites, very few entirely new patterns of organisation arose post-Ordovician; later evolution in trilobites was largely a matter of variations upon the Ordovician themes. By the Ordovician mass extinction vigorous trilobite radiation has stopped and gradual decline beckons.

Silurian and Devonian



Phacopid trilobite, Devonian age, Ohio, United States

Most Early Silurian families constitute a subgroup of the Late Ordovocian fauna. Few, if any, of the dominant Early Ordovician fauna survived to the end of the Ordovician, yet 74% of the dominant Late Ordovician trilobite fauna survived the Ordovician. Late Ordovician survivors account for all post-Ordovician trilobite groups except the Harpetida.

Silurian and Devonian trilobite assemblages are superficially similar to Ordovician assemblages, dominated by Lichida and Phacopida (including the well-known Calymenina). However, a number of characteristic forms do not extend far into the Devonian and almost all the remainder were wiped out by a series of drastic Middle and Late Devonian extinctions. Three orders and all but five families were exterminated by the combination of sea level changes and a break in the redox equilibrium (a meteorite impact has also been suggested as a cause). Only a single order, the Proetida, survived into the Carboniferous.

Carboniferous and Permian

The Proetida survived for millions of years, continued through the Carboniferous period and lasted until the end of the Permian (where the vast majority of species on Earth were wiped out). It is unknown why order Proetida alone survived the Devonian. The Proetida maintained relatively diverse faunas in deep water and shallow water, shelf environments throughout the Carboniferous. For many millions of years the Proetida existed untroubled in their ecological niche. An analogy would be today's crinoids which mostly exist as deep water species; in the Paleozoic era, vast 'forests' of crinoids lived in shallow near-shore environments.

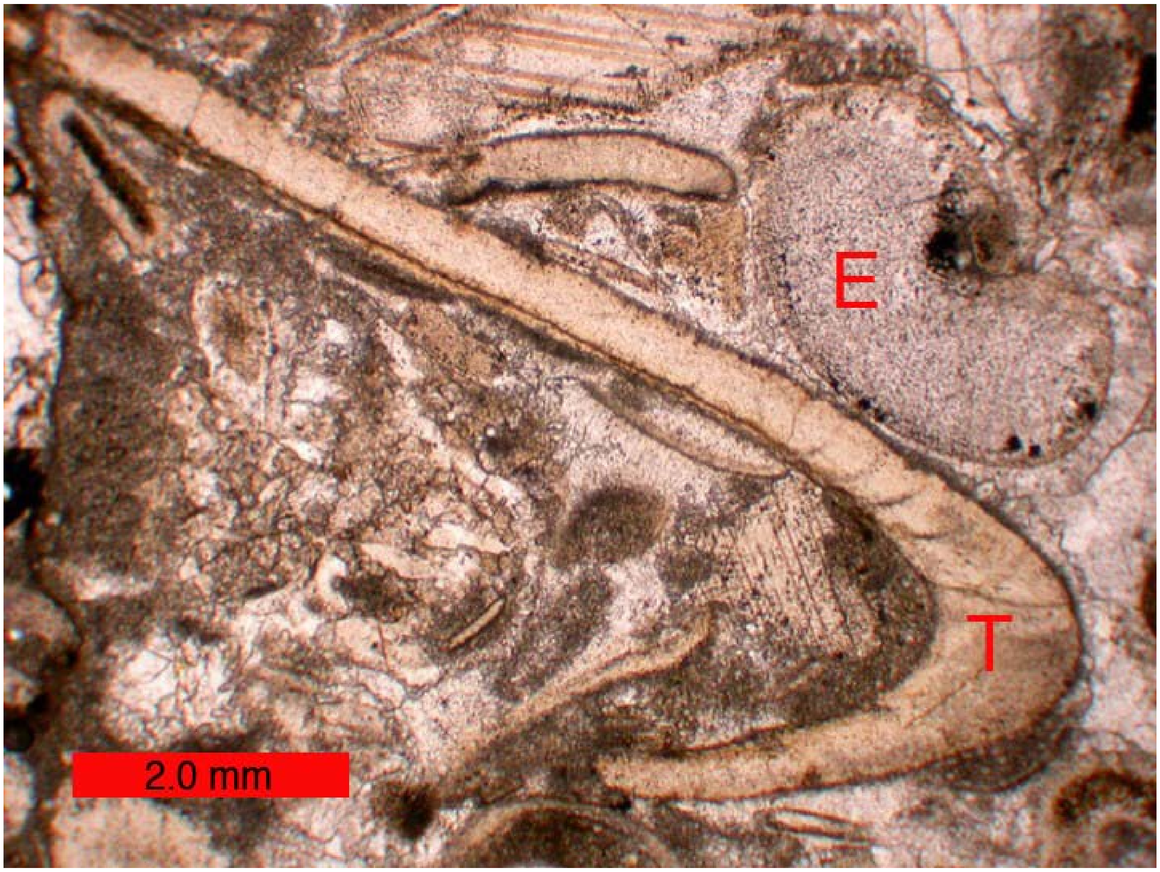
Final extinction

Exactly why the trilobites became extinct is not clear; with repeated extinction events (often followed by apparent recovery) throughout the trilobite fossil record, a combination of causes is likely. After the extinction event at the end of the Devonian period, what trilobite diversity remained was bottlenecked into the order Proetida. Decreasing diversity of genera limited to shallow water, shelf habitats coupled with a drastic lowering of sea level (regression) meant that the final decline of trilobites happened shortly before the end Permian mass extinction event. With so many marine species involved in the Permian extinction, the end of nearly 300 million successful years for the trilobite is hardly surprising.

The closest extant relatives of trilobites may be the horseshoe crabs, or the cephalocarids.

Fossil distribution

Cruziana, fossil trilobite furrowing trace



A trilobite fragment (T) in a thin-section of an Ordovician limestone; E=echinoderm; scale bar is 2 mm

Trilobites appear to have been exclusively marine organisms, since the fossilized remains of trilobites are always found in rocks containing fossils of other salt-water animals such as brachiopods, crinoids, and corals. Within the marine paleoenvironment, trilobites were found in a broad range from extremely shallow water to very deep water. Trilobites, like brachiopods, crinoids, and corals, are found on all modern continents, and occupied every ancient ocean from which Paleozoic fossils have been collected. The remnants of trilobites can range from the preserved body to pieces of the exoskeleton, which it sheds in the process known as ecdysis. In addition, the tracks left behind by trilobites living on the sea floor are often preserved as trace fossils.

There are three main forms of trace fossils associated with trilobites: *Rusophycus*; *Cruziana* & *Diplichnites* – such trace fossils represent the preserved life activity of trilobites active upon the sea floor. *Rusophycus*, the resting trace, are trilobite excavations which involve little or no forward movement and ethological interpretations suggest resting, protection and hunting. *Cruziana*, the feeding trace, are furrows through the sediment, which are believed to represent the movement of trilobites while deposit feeding. Many of the *Diplichnites* fossils are believed to be traces made by trilobites walking on the sediment surface. However, care must be taken as similar trace fossils are recorded in freshwater and post Paleozoic deposits, representing non-trilobite origins.

Trilobite fossils are found worldwide, with many thousands of known species. Because they appeared quickly in geological time, and moulted like other arthropods, trilobites serve as excellent index fossils, enabling geologists to date the age of the rocks in which they are found. They were among the first fossils to attract widespread attention, and new species are being discovered every year.

Rusophycus, a "resting trace" of a trilobite; Ordovician of southern Ohio. Scale bar is 10 mm.

A famous location for trilobite fossils in the United Kingdom is Wren's Nest, Dudley in the West Midlands, where *Calymene blumenbachi* is found in the Silurian Wenlock Group. This trilobite is featured on the town's coat of arms and was named the *Dudley Bug* or *Dudley Locust* by quarrymen who once worked the now abandoned limestone quarries. Llandrindod Wells, Powys, Wales, is another famous trilobite location. The well-known *Elrathia kingi* trilobite is found in abundance in the Cambrian age Wheeler Shale of Utah.

Spectacularly preserved trilobite fossils, often showing soft body parts (legs, gills, antennae, etc.) have been found in British Columbia, Canada (the Cambrian Burgess Shale and similar localities); New York State, U.S.A. (Ordovician Walcott-Rust quarry, near Russia, and Beecher's Trilobite Bed, near Rome); China (Lower Cambrian Maotianshan Shales near Chengjiang); Germany (the Devonian Hunsrück Slates near Bundenbach) and, much more rarely, in trilobite-bearing strata in Utah (Wheeler Shale and other formations), Ontario, and Manuels River, Newfoundland and Labrador.

Importance

The study of Paleozoic trilobites in the Welsh-English borders by Niles Eldredge was fundamental in formulating and testing punctuated equilibrium as a mechanism of evolution.

Identification of the 'Atlantic' and 'Pacific' trilobite faunas in North America and Europe implied the closure of the Iapetus Ocean (producing the Iapetus suture), thus providing important supporting evidence for the theory of continental drift.

Trilobites have been important in estimating the rate of speciation during the period known as the Cambrian Explosion because they are the most diverse group of metazoans known from the fossil record of the early Cambrian.

Trilobites are excellent stratigraphic markers of the Cambrian period: researchers who find trilobites with alimentary prosopon, and a micropygium, have found Early Cambrian strata. Most of the Cambrian stratigraphy is based on the use of trilobite marker fossils.

Trilobites are the state fossils of Ohio (*Isotelus*), Wisconsin (*Calymene celebra*) and Pennsylvania (*Phacops rana*).

Until the early 1900s, the Ute Indians of Utah wore trilobites, which they called *pachavee* (little water bug), as amulets. A hole was bored in the head and the fossil was worn on a string.

Chapter 5

Agnostida and Redlichiida

Agnostida

Agnostida Temporal range: Early Cambrian–Late Ordovician	
 *Peronopsis interstricta*	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	†Trilobita
Order:	**†Agnostida** Salter, 1864
Families	

Suborder Agnostina

- **Superfamily Agnostoidea**
  - Agnostidae
  - Ammagnostidae
  - Clavagnostidae
  - Diplagnostidae
  - Doryagnostidae

- Glyptagnostidae
- Metagnostidae
- Peronopsidae
- Ptychagnostidae
- Spinagnostidae

- **Superfamily Condylopygoidea**
  - Condylopygidae

Suborder Eodiscina

- **Superfamily Eodiscoidea**
  - Calodiscidae
  - Eodiscidae
  - Hebediscidae
  - Tsunyidiscidae
  - Weymouthiidae
  - Yukoniidae

Agnostida is an order of arthropod which first developed near the end of the Early Cambrian period and thrived during the Middle Cambrian. They are present in the lower Cambrian fossil record along with trilobites from the Redlichiida, Corynexochida, and Ptychopariida orders. The last agnostids went extinct in the Late Ordovician.

Systematics

The Agnostida are divided into two suborders — Agnostina and Eodiscina — that are then divided into a number of families. As a group, agnostids are isopygous, meaning that their pygidium is similar in size and shape to their cephalon. Most agnostid species were eyeless.

The systematic position of the order Agnostida within the class Trilobita remains uncertain, and there has been continuing debate whether they are trilobites or a stem group. The challenge to the status has focused on the Agnostina partly because juveniles of one genus have been found with legs greatly different from those of adult trilobites, suggesting they are not members of the lamellipedian clade, of which trilobites are a part. Instead, the limbs of agnostids closely resemble those of stem group crustaceans, although they lack the proximal endite, which defines that group. They are likely the sister taxon to the crustacean stem lineage, and, as such, part of the clade Crustaceomorpha. Other researchers have suggested, based on a cladistic analyses of dorsal exoskeletal features, that Eodiscina and Agnostida are closely united, and that the Eodiscina descended from the trilobite order Ptychopariida.

Ecology

Scientists have long debated whether the agnostids lived a pelagic or a benthic lifestyle. Their lack of eyes, a morphology not well-suited for swimming, and their fossils found in association with other benthic trilobites all suggest a benthic (bottom-dwelling) mode of life. They are likely to have lived on areas of the ocean floor that received little or no light and fed on detritus that descended from upper layers of the sea to the bottom. In contrast, their wide geographic dispersion in the fossil record is uncharacteristic of benthic animals, suggesting a pelagic existence. The thoracic segment appears to form a hinge between the head and pygidium allowing for a bivalved ostracodan-type lifestyle. Furthermore, the orientation of the thoracic appendages appears ill suited for benthic living.

They are sometimes preserved within the voids of other organisms, for instance within empty hyolith conchs, within sponges, worm tubes and under the carapaces of bivalved arthropods, presumably in order to hide from predators or strong storm currents; or maybe whilst scavenging for food. In the case of the tapering worm tubes *Selkirkia*, trilobites are always found with their heads directed towards the opening of the tube, suggesting that they reversed in; the absence of any moulted carapaces suggests that moulting was not their primary reason for seeking shelter.

Redlichiida

Redlichiida	

Redlichia takooensis , a member of the trilobite order Redlichiida.
Lower Cambrian Emu Shale
Kangaroo Island, South Australia

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Trilobita
Order:	**Redlichiida** Richter, 1932

Suborders

- Olenellina
- Redlichiina

Redlichiida is an order within the major extinct arthropod class Trilobita. The **Redlichids** are one of the four older classes of trilobites that originated in the Lower Cambrian.

Redlichid trilobites are the first arthropods to appear in the fossil record. The earliest known trilobite seems to be the genus *Fallotaspis*, which is a Redlichid. They are common fossils in Lower Cambrian faunas worldwide. They die out before the end of the Middle Cambrian. The two major Lagerstätten, at which Redlichids are found, are the Emu Bay shales of Southern Australia and the Maotianshan shales near Chengjiang in China.

Physical description

Redlichids look primitive. They typically have a large, semicircular cephalon and a highly-segmented thorax that tapers back to a small pygidium. Unlike many other trilobite orders, the Redlichids were probably not capable of defensive enrollment. The Redlichids generally have prominent, long, crescent-shaped eyes. They are often quite spiny with some or all of the following: genal, glabular, tail, segment spines. One Redlichid family, the Olenellids, typically have long spines on the third thoracic segment.

The appendages have been preserved in a few specimens. They follow typical trilobite patterns in terms of the number, placement, and types of legs, antennae, gills, etc.

Suborders

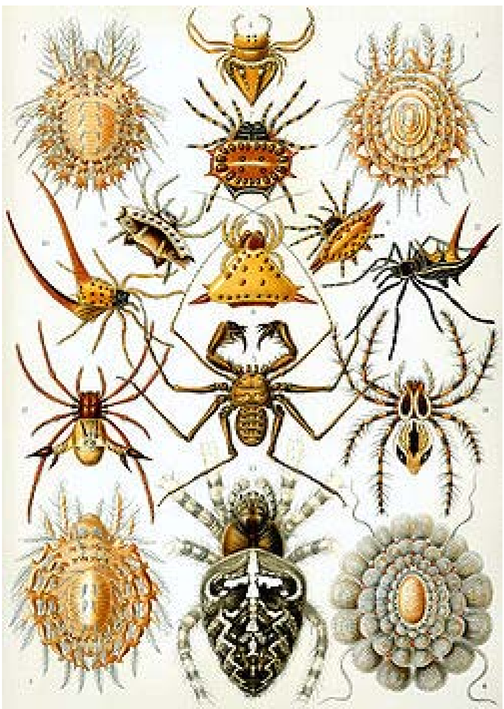
The Redlichiids are divided into two suborders: Olenellina and Redlichiina.

The Olenellids are found in North America and associated areas that comprised the Cambrian continent of Laurentia. They are very common and are used to define the scope of Laurentia. Their abrupt disappearance marks the Lower-Middle Cambrian boundary in areas where the Olenellids are found. Olenellids do not have a facial suture.

Members of suborder Redlichiina are associated with Cambrian regions other than Laurentia. They have facial sutures and their remains are frequently found without their *librigena*, or "free cheeks". The relatively uncommon Bathynotids had facial sutures, long genal spines, and long spines on the final thoracic segment.

Chapter 6

Arachnid

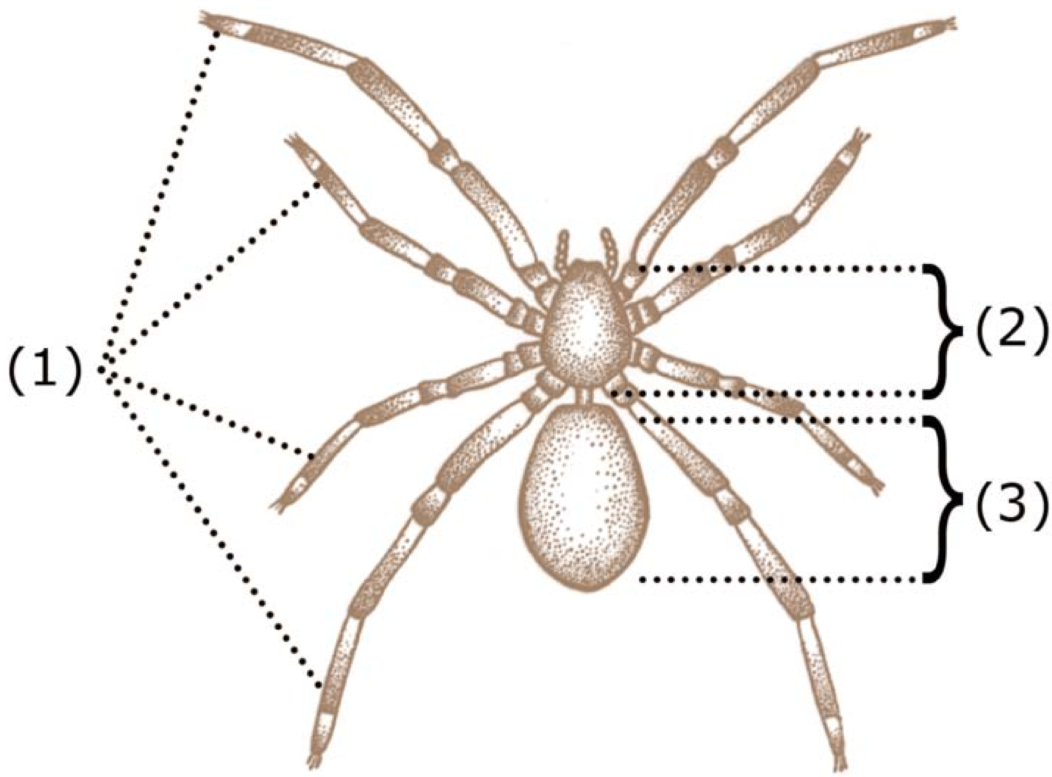
Arachnida **Temporal range: 420–0 Ma** **Silurian to Recent**	
	
"Arachnida" from Ernst Haeckel's *Kunstformen der Natur*, 1904	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	**Arachnida** Cuvier, 1812
Orders	
Acarina Amblypygi	

Araneae
†Haptopoda
Opiliones
Palpigradi
†Phalangiotarbida
Pseudoscorpionida
Ricinulei
Schizomida
Scorpiones
Solifugae
Thelyphonida
†Trigonotarbida

Arachnids are a class (**Arachnida**) of joint-legged invertebrate animals in the subphylum Chelicerata. All arachnids have eight legs, although in some species the front pair may convert to a sensory function. The term is derived from the Greek word ἀράχνη (*aráchnē*), meaning "spider".

Almost all extant arachnids are terrestrial. However, some inhabit freshwater environments and, with the exception of the pelagic zone, marine environments as well. They comprise over 100,000 named species, including spiders, scorpions, harvestmen, ticks, mites and Solifugae.

Anatomy



Basic characteristics of arachnids include four pairs of legs (1) and a body divided into two segments: the cephalothorax (2) and the abdomen (3).

Almost all adult arachnids have eight legs, and arachnids may be easily distinguished from insects by this fact, since insects have six legs. However, arachnids also have two further pairs of appendages that have become adapted for feeding, defense, and sensory perception. The first pair, the chelicerae, serve in feeding and defense. The next pair of appendages, the pedipalps have been adapted for feeding, locomotion, and/or reproductive functions. In Solifugae, the palps are quite leg-like, so that these animals appear to have ten legs. The larvae of mites and Ricinulei have only six legs; the fourth pair appears when they moult into nymphs. However, there are also adult mites with six, or even four legs.

Arachnids are further distinguished from insects by the fact they have no antennae or wings. Their body is organized into two tagma called the prosoma, or cephalothorax, and the opisthosoma, or abdomen. The cephalothorax is derived from the fusion of the cephalon (head) and the thorax, and is usually covered by a single, unsegmented carapace. The abdomen is segmented in the more primitive forms, but varying degrees of fusion between the segments occur in many groups. It is typically divided into a preabdomen and postabdomen, although this is only clearly visible in scorpions, and in some orders, such as the Acari, the abdominal sections are completely fused.

Like all arthropods, arachnids have an exoskeleton, and they also have an internal structure of cartilage-like tissue called the endosternite, to which certain muscle groups are attached. The endosternite is even calcified in some Opiliones.

Physiology

There are some characteristics that are particularly important for the terrestrial lifestyle of an arachnid, such as internal respiratory surfaces in the form of tracheae, or modification of the book gill into a book lung, an internal series of vascular lamellae used for gas exchange with the air. While the tracheae are often individual systems of tubes, similar to those in insects, ricnuleids, pseudoscorpions, and some spiders possess sieve tracheae, in which several tubes arise in a bundle from a small chamber connected to the spiracle. This type of tracheal system has almost certainly evolved from the book lungs, and indicates that the tracheae of arachnids are not homologous with those of insects.

Further adaptations to terrestrial life are appendages modified for more efficient locomotion on land, internal fertilisation, special sensory organs, and water conservation enhanced by efficient excretory structures as well as a waxy layer covering the cuticle.

The excretory glands of arachnids include up to four pairs of coxal glands along the side of the prosoma, and one or two pairs of Malpighian tubules, emptying into the gut. Many arachnids have only one or the other type of excretory gland, although several do have both. The primary nitrogenous waste product in arachnids is guanine.

The blood of arachnids is variable in composition, depending on the mode of respiration. Arachnids with an efficient tracheal system do not need to transport oxygen in the blood, and may have a reduced circulatory system. In scorpions and some spiders, however, the blood contains haemocyanin, a copper-based pigment with a similar function to haemoglobin in vertebrates. The heart is located in the forward part of the abdomen, and may or may not be segmented. Some mites have no heart at all.

Diet and digestive system

Arachnids are mostly carnivorous, feeding on the pre-digested bodies of insects and other small animals. Only in the harvestmen and among mites, such as the house dust mite, is there ingestion of solid food particles, and thus exposure to internal parasites, although it is not unusual for spiders to eat their own silk. Several groups secrete venom from specialized glands to kill prey or enemies. Several mites are parasites, some of which are carriers of disease.

Arachnids pour digestive juices produced in their stomachs over their prey after killing it with their pedipalps and chelicerae. The digestive juices rapidly turn the prey into a broth of nutrients which the arachnid sucks into a pre-buccal cavity located immediately in front of the mouth. Behind the mouth is a muscular, sclerotised pharynx, which acts as a pump, sucking the food through the mouth and on into the oesophagus and stomach. In some arachnids, the oesophagus also acts as an additional pump.

The stomach is tubular in shape, with multiple diverticula extending throughout the body. The stomach and its diverticula both produce digestive enzymes and absorb nutrients from the food. It extends through most of the body, and connects to a short sclerotised intestine and anus in the hind part of the abdomen.

Senses

Arachnids have two kinds of eyes, the lateral and median ocelli. The lateral ocelli evolved from compound eyes and may have a tapetum, which enhances the ability to collect light. The median ocelli develop from a transverse fold of the ectoderm. The ancestors of modern arachnids probably had both types, but modern ones often lack one type or the other. The cornea of the eye also acts as a lens, and is continuous with the cuticle of the body. Beneath this is a transparent vitreous body, and then the retina and, if present, the tapetum. In most arachnids, the retina probably does not have enough light sensitive cells to allow the eyes to form a proper image.

In addition to the eyes, almost all arachnids have two other types of sensory organs. The most important to most arachnids are the fine sensory hairs that cover the body and give the animal its sense of touch. These can be relatively simple, but many arachnids also possess more complex structures, called trichobothria.

Finally, slit sense organs are slit-like pits covered with a thin membrane. Inside the pit, a small hair touches the underside of the membrane, and detects its motion. Slit sense organs are believed to be involved in proprioception, and possibly also hearing.

Reproduction

Arachnids may have one or two gonads, which are located in the abdomen. The genital opening is usually located on the underside of the second abdominal segment. In most species, the male transfers sperm to the female in a package, or spermatophore. Complex courtship rituals have evolved in many arachnids to ensure the safe delivery of the sperm to the female.

Arachnids usually lay yolky eggs, which hatch into immatures that resemble adults. Scorpions, however, are either ovoviviparous or viviparous, depending on species, and bear live young.

Systematics

- † Trigonotarbida — extinct
- Amblypygi — "blunt rump" tailless whip scorpions with front legs modified into whip-like sensory structures as long as 25 cm or more (140 species)

- Araneae — true spiders (40,000 species)
    - Mesothelae — very rare, basal spiders, with abdomen segmented and spinnerets median
    - Opisthothelae — spiders with abdomen unsegmented and spinnerets located posteriorly
        - Araneomorphae — most common spiders
        - Mygalomorphae — tarantulas and tarantula-like spiders
- † Phalangiotarbida — extinct
- Opiliones — phalangids, harvestmen or daddy-long-legs (6,300 species)
- Palpigradi — microwhip scorpions (80 species)
- Pseudoscorpionida — pseudoscorpions (3,000 species)
- Ricinulei — ricinuleids, hooded tickspiders (60 species)
- Schizomida — "split middle" whip scorpions with divided exoskeletons (220 species)
- Scorpiones — scorpions (2,000 species)
- Solifugae — solpugids, windscorpions, sun spiders or camel spiders (900 species)
- † Haptopoda — extinct
- Thelyphonida — vinegarroons or whip scorpions (formerly uropygida) forelegs modified into sensory appendages and a long tail on abdomen tip (100 species)
- Acarina — mites and ticks (30,000 species)
    - Acariformes
        - Sarcoptiformes
        - Trombidiformes
    - Opilioacariformes
    - Parasitiformes — holothyrans, ticks and mesostigmatic mites

It is estimated that a total of 98,000 arachnid species have been described, and that there may be up to 600,000 in total, including undescribed species.

Acarina

Ixodes hexagonus, a tick

Acarina or **Acari** is a taxon of arachnids that contains mites and ticks. Its fossil history goes back to the Devonian period, although there is also a questionable Ordovician record. The Devonian period was the time frame in which certain species of animals developed legs. In most modern treatments, the Acari is considered a subclass of Arachnida and is composed of 2–3 orders or superorders: Acariformes, Parasitiformes, and Opilioacariformes. Most acarines are minute to small (e.g. 0.080–1.00 mm), but the giants of the Acari (some ticks and red velvet mites) may reach lengths of 10–20 mm. It is estimated that over 50,000 species have been described (as of 1999) and that a million or more species are currently living. The study of mites and ticks is called acarology.

Only the faintest traces of primary segmentation remain in mites, the prosoma and opisthosoma being insensibly fused, and a region of flexible cuticle (the cirumcapitular furrow) separates the chelicerae and pedipalps from the rest of the body. This anterior body region is called the gnathosoma (or capitulum) and is also found in the Ricinulei. The remainder of the body is called the idiosoma and is unique to mites. Most adult mites have four pairs of legs, like other arachnids, but some have fewer. For example, gall mites like *Phyllocoptes variabilis* (superfamily Eriophyioidea) have a wormlike body with only two pairs of legs; some parasitic mites have only one or three pairs of legs in the adult stage. Larval and prelarval stages have a maximum of three pairs of legs; adult mites with only three pairs of legs may be called 'larviform'.

Acarine ontogeny consists of an egg, a prelarval stage (often absent), a larval stage (hexapod except in Eriophyoidea, which have only 2 pairs of legs), and a series of nymphal stages. Larvae (and prelarvae) have a maximum of 3 pairs of legs (legs are often reduced to stubs or absent in prelarvae); legs IV are added at the first nymphal stage.

Acarines live in practically every habitat, and include aquatic (freshwater and sea water) and terrestrial species. They outnumber other arthropods in the soil organic matter and detritus. Many are parasitic, and they affect both vertebrates and invertebrates. Most parasitic forms are external parasites, while the free living forms are generally predaceous and may even be used to control undesirable arthropods. Others are detritivores that help to break down forest litter and dead organic matter such as skin cells. Others still are plant feeders and may damage crops. Damage to crops is perhaps the most costly economic effect of mites, especially by the spider mites and their relatives (Tetranychoidea), earth mites (Penthaleidae), thread-footed mites (Tarsonemidae) and the gall and rust mites (Eriophyoidea). Some parasitic forms affect humans and other mammals, causing damage by their feeding, and can even be vectors of diseases such as scrub typhus and rickettsial pox. A well-known effect of mites on humans is their role as an allergen and the stimulation of asthma in people affected by the respiratory disease. The use of predatory mites (e.g. Phytoseiidae) in pest control and herbivorous mites that attack weeds is also important. An unquantified, but major positive contribution of the Acari is their normal functioning in ecosystems, especially their roles in the decomposer subsystem.

Amblypygi

An amblypygid

Amblypygids are also known as **tailless whip scorpions** or **cave spiders**. Approximately 5 families, 17 genera and 136 species have been described. They are found in tropical and subtropical regions worldwide. Some species are subterranean; many are nocturnal. During the day, they may hide under logs, bark, stones, or leaves. They prefer a humid environment. Amblypygids may range from 5 to 40 mm. Their bodies are broad and highly flattened and the first pair of legs (the first walking legs in most arachnid orders) are modified to act as sensory organs. (Compare solifugids, uropygids, and schizomids.) These very thin modified legs can extend several times the length of body. They have no silk glands or venomous fangs, but can have prominent pincer-like pedipalps. Amblypygids often move about sideways on their six walking legs, with one "whip" pointed in the direction of travel while the other probes on either side of them. Prey are located with these "whips", captured with pedipalps, then torn to pieces with chelicerae. Fossilised amblypygids have been found dating back to the Carboniferous period.

Amblypygids, particularly the species *Phrynus marginemaculatus* and *Damon diadema*, are thought to be one of the few species of arachnids that show signs of social behavior. Research conducted at Cornell University by entomologists suggests that mother amblypygids comfort their young by gently caressing the offspring with her feelers. Further, when two or more siblings were placed in an unfamiliar environment, such as a cage, they would seek each other out and gather back in a group.

Araneae

Araneus diadematus

Araneae, or spiders, are the most familiar of the arachnids, and the most numerous, if only described species are counted. All spiders produce silk, a thin, strong protein strand extruded by the spider from spinnerets most commonly found on the end of the abdomen. Many species use it to trap insects in webs, although there are many species that hunt freely. Silk can be used to aid in climbing, form smooth walls for burrows, build egg sacs, wrap prey, temporarily hold sperm, and even fly, among other applications.

All spiders except those in the families Uloboridae and Holarchaeidae, and in the suborder Mesothelae (together about 350 species) can inject venom to protect themselves or to kill and liquefy prey. Only about 200 species, however, have bites that can pose health problems to humans. Many larger species' bites may be painful, but will not produce lasting health concerns.

Spiders are found all over the world, from the tropics to the Arctic, with some extreme species even living underwater in silken domes that they supply with air, and on the tops of the highest mountains.

Haptopoda

Haptopoda is an extinct order known exclusively from a few specimens from the Upper Carboniferous of the United Kingdom. It is monotypic, i.e. has only one species: *Plesiosiro madeleyi* Pocock 1911. Relationships with other arachnids are obscure, but closest relatives may be the Amblypygi, Thelyphonida and Schizomida of the tetrapulmonate clade.

Opiliones

Paroligolophus agrestis

Opiliones (formerly *Phalangida*, and better known as "**harvestmen**" or "**daddy longlegs**") are arachnids that are harmless to people and are known for their exceptionally long walking legs, compared to their body size. As of 2007, over 6,400 species of Phalangids have been discovered worldwide. The order Opiliones is divided into four suborders: Cyphophthalmi, Eupnoi, Dyspnoi and Laniatores. Well-preserved fossils have been found in the 410-million year old Rhynie cherts of Scotland; they look surprisingly modern, suggesting that the basic structure of the harvestmen has not changed much since then.

The difference between harvestmen and spiders is that in harvestmen the two main body sections (the abdomen or *opisthosoma* with ten segments and the cephalothorax or *prosoma*) are nearly joined, so that they appear to be one oval structure. In more advanced species, the first five abdominal segments are often fused into a dorsal shield called the scutum, which is normally fused with the carapace. Sometimes this shield is only present in males. The two hindmost abdominal segments may be reduced or separated in the middle on the surface to form two plates lying next to each other. The second pair of legs is longer than the others and works as antennae. They have a single pair of eyes in the middle of their heads, orientated sideways. They have a pair of prosomatic scent glands that secrete a peculiar smelling fluid when disturbed. Harvestmen do not have silk glands and do not possess poison glands, posing absolutely no danger to humans. They breathe through tracheae. Between the base of the fourth pair of legs and the abdomen is a pair of spiracles, one opening on each side. In more active species, spiracles are also found upon the tibia of the legs. They have a gonopore on the ventral cephalothorax, and copulation is direct, as the male has a penis (while the female has an ovipositor).

Typical body length does not exceed 7 mm (about ¼ in) even in the largest species. However, leg span is much larger and can exceed 160 mm (over 6 in). Most species live for a year. Many species are omnivorous, eating primarily small insects and all kinds of plant material and fungi; some are scavengers of the decays of any dead animal, bird dung and other fecal material. They are mostly nocturnal and coloured in hues of brown, although there are a number of diurnal species that have vivid patterns in yellow, green and black with varied reddish and blackish mottling and reticulation.

Palpigradi

Palpigradi, commonly known as "microwhip scorpions", are tiny cousins of the uropygid, or whip scorpion, no more than 3 mm in length. They have a thin, pale, segmented carapace that terminates in a whip-like flagellum, made up of 15 segments. The carapace is divided into two plates between the third and fourth leg set. They have no eyes. Some species have three pairs of book lungs, while others have no respiratory organs at all. Approximately 80 species of Palpigradi have been described worldwide, in the families Eukoeneniidae and Prokoeneniidae, with a total of seven genera.

They are believed to be predators like their larger relatives, feeding on minuscule insects in their habitat. Their mating habits are unknown, except that they lay only a few relatively large eggs at a time. Microwhip scorpions need a damp environment to survive, and they always hide from light, so they are commonly found in the moist earth under buried stones and rocks. They can be found on every continent, except in Arctic and Antarctic regions.

Phalangiotarbida

Phalangiotarbi (Haase, 1890) is an extinct arachnid order known exclusively from the Palaeozoic (Devonian to Permian) of Europe and North America.

The affinities of phalangiotarbids are obscure, with most authors favouring affinities with Opiliones (harvestmen) and/or Acari (mites and ticks). Phalangiotarbida has been recently proposed to be sister group to (Palpigradi+Tetrapulmonata): the taxon Megoperculata sensu Shultz (1990). (Pollitt et al., 2004).

Pseudoscorpions

A pseudoscorpion on a printed page

Pseudoscorpions are small arthropods with a flat, pear-shaped body and pincers that resemble those of scorpions. They range from 2 to 8 mm (1/12 to 1/3 inch) in length. The opisthosoma is made up of twelve segments, each guarded by plate-like tergites above and sternites below. The abdomen is short and rounded at the rear, rather than extending into a segmented tail and stinger like true scorpions. The colour of the body can be yellowish-tan to dark-brown, with the paired claws often a contrasting colour. They may have two, four or no eyes. They have two very long *palpal chelae* (pedipalps or pincers) that strongly resemble the pincers found on a scorpion. The pedipalps generally consist of an immobile "hand" and "finger", with a separate movable finger controlled by an adductor muscle. A venom gland and duct are usually located in the mobile finger; the poison is used to capture and immobilise the pseudoscorpion's prey. During digestion, pseudoscorpions pour a mildly corrosive fluid over the prey, then ingest the liquefied remains. Pseudoscorpions spin silk from a gland in their jaws to make disk-shaped cocoons for mating, molting, or waiting out cold weather. Another trait they share with their closest relatives, the spiders, is breathing through spiracles. Most spiders have one pair of spiracles, and one of book lungs, but pseudoscorpions do not have book lungs.

There are more than 2,000 species of pseudoscorpions recorded. They range worldwide, even in temperate to cold regions, but have their most dense and diverse populations in the tropics and subtropics. The fossil record of pseudoscorpions dates back over 380 million years, to the Devonian period, near the time when the first land-animal fossils appear.

During the elaborate mating dance, the male of some pseudoscorpion species pulls a female over a spermatophore previously laid upon a surface. In other species, the male also pushes the sperm into the female genitals using the forelegs. The female carries the fertilised eggs in a brood pouch attached to her abdomen, and the young ride on the mother for a short time after they hatch. Up to two dozen young are hatched in a single brood; there may be more than one brood per year. The young go through three molts over the course of several years before reaching adulthood. Adult pseudoscorpions live 2 to 3 years. They are active in the warm months of the year, overwintering in silken cocoons when the weather grows cold.

Pseudoscorpions are generally beneficial to humans since they prey on clothes moth larvae, carpet beetle larvae, booklice, ants, mites, and small flies. They are small and inoffensive, and are rarely seen due to their size. They usually enter the home by "riding along" with larger insects (known as phoresy), or are brought in with firewood. They are often observed in bathrooms or laundry rooms, since they seek humidity. They may sometimes be found feeding on mites under the wing covers of certain beetles.

Ricinulei

Riniculei (*hooded tickspiders*) are 5–10 mm long. Their most notable feature is a "hood" that can be raised and lowered over the head; when lowered, it covers the mouth and the chelicerae. Ricinulei have no eyes. The pedipalps end in pincers that are small relative to their bodies, when compared to those of the related orders of scorpions and pseudoscorpions. The heavy-bodied abdomen forms a narrow pedicel, or waist, where it attaches to the prosoma. In males, the third pair of legs are modified to form copulatory organs. Malpighian tubules and a pair of coxal glands make up the excretory system. They have no lungs, as gas exchange takes place through the trachea.

Ricinulei are predators, feeding on other small arthropods. Little is known about their mating habits; the males have been observed using their modified third leg to transfer a spermatophore to the female. The eggs are carried under the mother's hood, until the young hatch into six-legged "larva", which later molt into their adult forms. Ricinulei require moisture to survive. Approximately 57 species of ricinuleids have been described worldwide, all in a single family that contains 3 genera.

Schizomida

Schizomida is an order of arachnids that tend to live in the top layer of soils. Schizomids present the prosoma covered by a large protopeltidium and smaller, paired, mesopeltidia and metapeltidia. There are no eyes. The opisthosoma is a smooth oval of 12 recognisable somites. The first is reduced and forms the pedicel. The last three are much constricted, forming the pygidium. The last somite bears the flagellum, which in this order is short and consists of not more than four segments.

The name means "split or cleaved middle", referring to the way the cephalothorax is divided into two separate plates. Like the related orders Uropygi, Amblypygi, and Solpugida, the schizomids use only six legs for walking, having modified their first two legs to serve as sensory organs. They also have large well-developed pedipalps (pincers) just behind the sensory legs.

Scorpions

Scorpio maurus palmatus

Scorpions are characterised by a metasoma (tail) comprising six segments, the last containing the scorpion's anus and bearing the telson (the sting). The telson, in turn, consists of the vesicle, which holds a pair of venom glands and the hypodermic aculeus, the venom-injecting barb. The abdomen's front half, the mesosoma, is made up of six segments. The first segment contains the sexual organs as well as a pair of vestigial and modified appendages forming a structure called the genital operculum. The second segment bears a pair of featherlike sensory organs known as the *pectines*; the final four segments each contain a pair of book lungs. The mesosoma is armored with chitinous plates, known as tergites on the upper surface and sternites on the lower surface.

The cuticle of scorpions is covered with hairs in some places that act like balance organs. An outer layer that makes them fluorescent green under ultraviolet light is called the hyaline layer. Newly molted scorpions do not glow until after their cuticle has hardened. The fluorescent hyaline layer can be intact in fossil rocks that are hundreds of millions of years old.

Scorpions are opportunistic predators of small arthropods and insects. They use their chela (pincers) to catch the prey initially. Depending on the toxicity of their venom and size of their claws, they will then either crush the prey or inject it with neurotoxic venom. The neurotoxins consist of a variety of small proteins as well as sodium and potassium cations, which serve to interfere with neurotransmission in the victim. Scorpions use their venom to kill or paralyze their prey so that it can be eaten; in general it is fast acting, allowing for effective prey capture. Scorpion venoms are optimised for action upon other arthropods and therefore most scorpions are relatively harmless to humans; stings produce only local effects (such as pain, numbness or swelling). A few scorpion species, however, mostly in the family Buthidae, can be dangerous to humans. The scorpion that is responsible for the most human deaths is the *Androctonus australis*, or fat-tailed scorpion of North Africa. The toxicity of *A. australis*'s venom is roughly half that of the deathstalker (*Leiurus quinquestriatus*), but since *A. australis* injects quite a bit more venom into its prey, it is the most deadly to humans. Human deaths normally occur in the young, elderly, or infirm; scorpions are generally unable to deliver enough venom to kill healthy adults. Some people, however may be allergic to the venom of some species, in which case the scorpion's sting can more likely kill. A primary symptom of a scorpion sting is numbing at the injection site, sometimes lasting for several days. It has been found that scorpions have two types of venom: a translucent, weaker venom designed to stun only, and an opaque, more potent venom designed to kill heavier threats.

Unlike the majority of Arachnida species, scorpions are viviparous. The young are born one by one, and the brood is carried about on its mother's back until the young have undergone at least one moult. The young generally resemble their parents, requiring between five and seven moults to reach maturity. Scorpions have quite variable lifespans and the lifespan of most species is not known. The age range appears to be approximately 4–25 years (25 years being the maximum reported life span in the giant desert hairy scorpion (*Hadrurus arizonensis*)). They are nocturnal and fossorial, finding shelter during the day in the relative cool of underground holes or undersides of rocks and coming out at night to hunt and feed. Scorpions prefer to live in areas where the temperatures range from 20°C to 37 °C (68°F to 99 °F), but may survive in the temperature range of 14 °C to 45 °C (57 °F to 113 °F).

Scorpions have been found in many fossil records, including coal deposits from the Carboniferous Period and in marine Silurian deposits. They are thought to have existed in some form since about 425–450 million years ago. They are believed to have an oceanic origin, with gills and a claw like appendage that enabled them to hold onto rocky shores or seaweed.

Solifugae

Galeodes sp.

Solifugae is a group of 900 species of arachnids, commonly known as *camel spiders*, *wind scorpions*, and *sun spiders*. The name derives from Latin, and means *those that flee from the sun*. Most Solifugae live in tropical or semitropical regions where they inhabit warm and arid habitats, but some species have been known to live in grassland or forest habitats. The most distinctive feature of Solifugae is their large chelicerae. Each of the two chelicerae are composed of two articles forming a powerful pincer; each article bears a variable number of teeth. Males in all families but Eremobatidae possess a flagellum on the basal article of the chelicera. Solifugae also have long pedipalps, which function as sense organs similar to insects' antennae and give the appearance of the two extra legs. Pedipalps terminate in reversible adhesive organs.

Solifugae are carnivorous or omnivorous, with most species feeding on termites, darkling beetles, and other small arthropods; however, solifugae have been videotaped consuming larger prey such as lizards. Prey is located with the pedipalps and killed and cut into pieces by the chelicerae. The prey is then liquefied and the liquid ingested through the pharynx. Reproduction can involve direct or indirect sperm transfer; when indirect, the male emits a spermatophore on the ground and then inserts it with his chelicerae in the female's genital pore.

Trigonotarbida

The Order **Trigonotarbida** is an extinct group of arachnids whose fossil record extends from the Silurian to the Lower Permian. They are known from several localities in northern asia, North America and Argentina. They superficially resemble spiders, to which they were clearly related.

These early arachnids seem to have been adapted to stalking prey on the ground. They have been found within the very structure of ground-dwelling plants, possibly where they hid to await their prey. Trigonotarbids are currently among the oldest known land arthropods. They lack silk glands on the opisthosoma and cheliceral poison glands, and most likely represented independent offshoots of the Arachnida.

Thelyphonida

A whip scorpion

The **Thelyphonida** (formerly **Uropygida**), commonly known as *vinegarroons* or *whip scorpions*, range from 25 to 85 mm in length; the largest species, of the genus *Mastigoproctus*, reaches 85 mm. Like the related orders Schizomida, Amblypygi, and Solifugae, the vinegarroons use only six legs for walking, having modified their first two legs to serve as antennae-like sensory organs. Many species also have very large scorpion-like pedipalps (pincers). They have one pair of eyes at the front of the cephalothorax and three on each side of the head. Whip scorpions have no poison glands, but they do have glands near the rear of their abdomen that can spray a combination of acetic acid and octanoic acid when they are bothered. Other species spray formic acid or chlorine. As of 2006, over 100 species have been described worldwide.

Whip scorpions are carnivorous, nocturnal hunters feeding mostly on insects but sometimes on worms and slugs. The prey is crushed between special teeth on the inside of the trochanters (the second segment of the leg) of the front legs. They are valuable in controlling the population of roaches and crickets.

Males secrete a sperm sac, which is transferred to the female. Up to 35 eggs are laid in a burrow, within a mucous membrane that preserves moisture. Mothers stay with the eggs and do not eat. The white young that hatch from the eggs climb onto their mother's back and attach themselves there with special suckers. After the first molt they look like miniature whip scorpions, and leave the burrow; the mother dies soon after. The young grow slowly, going through three molts in about three years before reaching adulthood.

Vinegarroons are found in tropical and subtropical areas worldwide, usually in underground burrows that they dig with their pedipalps. They may also burrow under logs, rotting wood, rocks, and other natural debris. They enjoy humid, dark places and avoid the light.

Chapter 7

Sea Spider

Sea spiders **Temporal range: Late Cambrian–Recent**	

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	**Pycnogonida** Latreille, 1810
Order:	**Pantopoda** Gerstaecker, 1863

Families

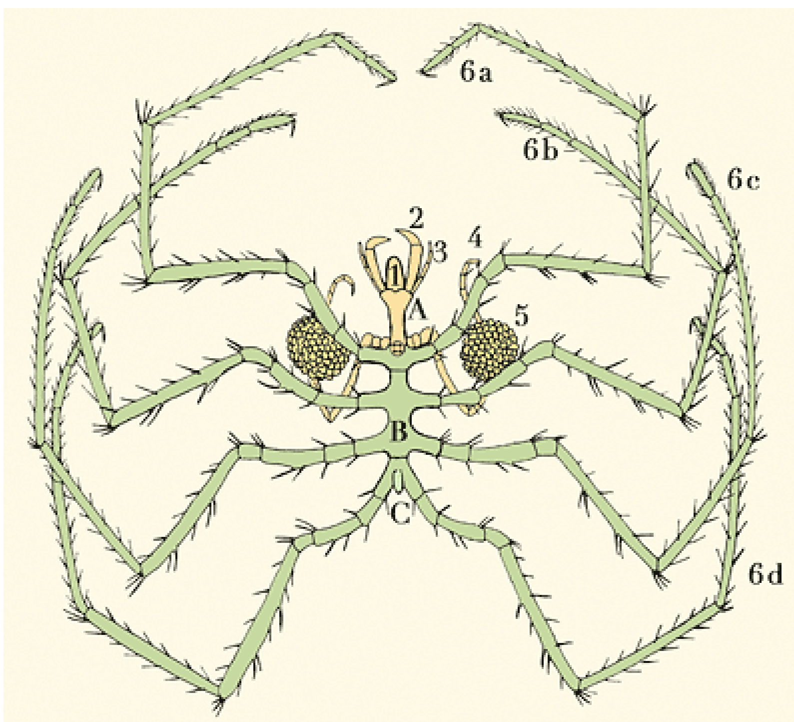
- Ammotheidae
- Austrodecidae
- Callipallenidae
- Colossendeidae
- Endeididae
- Nymphonidae
- Pallenopsidae
- Phoxichilidiidae

- Pycnogonidae
- Rhynchothoracidae

Sea spiders, also called **Pantopoda** or **pycnogonids**, are marine arthropods of class **Pycnogonida**. They are cosmopolitan, found especially in the Mediterranean and Caribbean Seas, as well as the Arctic and Antarctic Oceans. There are over 1300 known species, ranging in size from 1 to 10 millimetres (0.039 to 0.39 in) to over 90 cm (35 in) in some deep water species. Most are toward the smaller end of this range in relatively shallow depths, however, they can grow to be quite large in Antarctic waters.

Although "sea spiders" are not true spiders, or even arachnids, and should not be confused with Water Spiders, their traditional classification as chelicerates would place them closer to true spiders than to other well known arthropod groups, such as insects or crustaceans. However this is in dispute, as genetic evidence suggests they may even be an ancient sister group to all other living arthropods.

Description



Anatomy of a pycnogonid:
A: head; **B**: thorax; **C**: abdomen
1: proboscis; **2**: chelifores; **3**: palps; **4**: ovigers; **5**: egg sacs; **6a–6d**: four pairs of legs

Sea spiders have long legs in contrast to a small body size. The number of walking legs is usually eight (four pairs), but species with five and six pairs exist. Because of their small size and slender body and legs, no respiratory system is necessary, with gases moving by diffusion. A proboscis allows them to suck nutrients from soft-bodied invertebrates, and their digestive tract has diverticula extending into the legs.

Pycnogonids are so small that each of their tiny muscles consists of only one single cell, surrounded by connective tissue. The anterior region consists of the proboscis, which has fairly limited dorsoventral and lateral movement, and three to four appendages including the ovigers, which are used in caring for young and cleaning as well as courtship. In some species, the chelifores, palps and ovigers can be reduced or missing in adults. In those species that lack chelifores and palps, the proboscis is well developed and more mobile and flexible, often equipped with numerous sensory bristles and strong rasping ridges around the mouth. The last segment includes the anus and tubercle, which projects dorsally.

In total, pycnogonids have four to six pairs of legs for walking as well as other appendages which often resemble legs. A cephalothorax and much smaller abdomen make up the extremely reduced body of the pycnogonid, which has up to two pairs of dorsally located simple eyes on its non-calcareous exoskeleton, though sometimes the eyes can be missing, especially among species living in the deep oceans. The abdomen does not have any appendages, and in most species it is reduced and almost vestigial. The organs of this chelicerate extend throughout many appendages because its body is too small to accommodate all of them alone.

The morphology of the sea spider creates an extremely well-suited surface-area to volume ratio for any respiration to occur through direct diffusion. The most recent research seems to indicate that waste leaves the body through the digestive tract or is lost during a moult. The small, long, thin pycnogonid heart beats vigorously at 90 to 180 beats per minute, creating substantial blood pressure. These creatures possess an open circulatory system as well as a nervous system consisting of a brain which is connected to two ventral nerve cords, which in turn connect to specific nerves.

Reproduction and development

All pycnogonid species have separate sexes except for one species that is hermaphroditic. Females possess a pair of ovaries, while males possess a pair of testes located dorsally in relation to the digestive tract. Reproduction involves external fertilisation after “a brief courtship”, but very little is known about the secret lives of most pycnogonids. Only males care for laid eggs and young.

The larva has a blind gut and the body consist literally of a head and its three pairs of cephalic appendages only: the chelifores, palps and ovigers. The abdomen and the thorax with its thoracic appendages develops later. One theory is that this reflects how a common ancestor of all arthropods evolved; starting its life as a small animal with a pair of appendages used for feeding and two pairs used for locomotion, while new segments and segmental appendages were gradually added as it was growing.

At least four types of larvae have been described: the typical protonymphon larva, the encysted larva, the atypical protonymphon larva, and the attaching larva. The typical protonymphon larva is most common, is free living and gradually turns into an adult. The encysted larva is a parasite that hatches from the egg and finds a host in the shape of a polyp colony where it burrows into and turns into a cyst, and will not leave the host before it has turned into a young juvenile.

Not much is known about the development of the atypical protonymphon larva. The adults are free living, while the larvae and the juveniles are living on or inside temporary hosts such as polychaetes and clams. When the attaching larva hatches it still looks like an embryo, and immediately attaches itself to the ovigerous legs of the father, where it will stay until it has turned into a small and young juvenile with two or three pairs of walking legs ready for a free-living existence.

Distribution and ecology

A pycnogonid in its natural habitat

These small animals live in many different parts of the world, from Australia, New Zealand, and the Pacific coast of the United States, to the Mediterranean Sea and the Caribbean Sea, to the north and south poles. They are most common in shallow waters, but can be found as deep as 7,000 metres (23,000 ft), and live in both marine and estuarine habitats. Pycnogonids are well camouflaged beneath the rocks and among the algae that are found along shorelines.

Sea spiders either walk along the bottom with their stilt-like legs or swim just above it using an umbrella pulsing motion. Most are carnivorous and feed on cnidarians, sponges, polychaetes and bryozoans. Sea spiders are generally predators or scavengers. They will often insert their proboscis, a long appendage used for digestion and sucking food into its gut, into a sea anemone and suck out nourishment. The sea anemone, large in comparison to its predator, almost always survives this ordeal.

Classification

The class Pycnogonida comprises over approximately 1,300 species, which are normally split into eighty-six genera. The correct taxonomy within the group is uncertain, and it appears that no agreed list of orders exists. Accordingly, families are listed in the taxobox, all considered part of the single order Pantopoda.

Sea spiders have long been considered to belong to the Chelicerata, together with horseshoe crabs, true spiders, mites, ticks and scorpions.

Another idea is that they belong to their own lineage, distinct from chelicerates, crustaceans, myriapods, or insects. The reason for this is that it seems the appendages called chelifores are unique among extant arthropods, and are not homologous to the chelicerae in real chelicerates as previously supposed. Instead of developing from the deuterocerebrum, they can be traced to the protocerebrum, the anterior part of the arthropod brain and found in the first head segment that in all other arthropods give rise to the eyes only. This is not found anywhere else among arthropods except in some fossil forms like *Anomalocaris*, indicating that the Pycnogonida may be a sister group to all other living arthropods, the latter having evolved from some ancestor that had lost the protocerebral appendages. If this is confirmed, it would mean the sea spiders are the last surviving (and highly modified) members of an ancient stem group of arthropods that lived in Cambrian oceans.

Recent work places the Pycnogonida outside the Arachnomorpha as basal Euarthropoda, or inside Chelicerata (based on the chelifore-chelicera putative homology).

Fossil record

Although the fossil record of pycnogonids is scant, it is clear that they once possessed a coelom, but it was later lost, and that the group is very old.

The earliest fossils are known from the Cambrian 'Orsten' of Sweden, the Silurian Wenlock Series of England and the Devonian Hunsrück Slate of Germany. Some of these specimens are significant in that they possess a longer 'trunk' behind the abdomen and in two fossils the body ends in a tail; something never seen in living sea spiders.

In 2007 remarkably well-preserved fossils were exposed in fossil beds at La Voulte-sur-Rhône, near Lyon in south-eastern France. Researchers from the University of Lyon discovered about 70 fossils from three distinct species in the 160 million-year-old Jurassic La Voulte Lagerstätte. The find will help fill in an enormous gap in the history of these creatures.

Chapter 8

Centipede

Centipedes Temporal range: 418–0 Ma Late Silurian to Recent	

Scolopendra sp. (Scolopendromorpha: Scolopendridae)

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Myriapoda
Class:	**Chilopoda** Latreille, 1817

Orders and Families

Scutigeromorpha

- Pselliodidae
- Scutigeridae
- Scutigerinidae

Lithobiomorpha

- Henicopidae
- Lithobiidae

Craterostigmomorpha

- Craterostigmidae

Scolopendromorpha

- Cryptopidae
- Scolopendridae
- Scolopocryptopidae

Geophilomorpha

- Mecistocephalidae
- Neogeophilidade
- Geophilidae
- Geophilidae
- Linotaeniidae

Centipedes (from Latin prefix *centi*-, "hundred", and *pes*, *pedis*, "foot") are arthropods belonging to the class **Chilopoda** of the subphylum Myriapoda. They are elongated metameric animals with one pair of legs per body segment. Despite the name, centipedes can have a varying number of legs from under 20 to over 300. Centipedes have an odd number of pairs of legs, e.g. 15 or 17 pairs of legs (30 or 34 legs) but never 16 pairs (32 legs). A key trait uniting this group is a pair of venom claws or "forcipules" formed from a modified first appendage. Centipedes are a predominantly carnivorous taxon.

Centipedes normally have a drab coloration combining shades of brown and red. Cavernicolous (cave-dwelling) and subterranean species may lack pigmentation and many tropical scolopendromorphs have bright aposematic colours. Size can range from a few millimetres in the smaller lithobiomorphs and geophilomorphs to about 30 cm (12 in) in the largest scolopendromorphs. Centipedes can be found in a wide variety of environments.

Worldwide there are estimated to be 8,000 species of centipede, of which 3,000 have been described. Centipedes have a wide geographical range, reaching beyond the Arctic Circle. Centipedes are found in an array of terrestrial habitats from tropical rainforests to deserts. Within these habitats centipedes require a moist micro-habitat because they lack the waxy cuticle of insects and arachnids, and so lose water rapidly through the skin. Accordingly, they are found in soil and leaf litter, under stones and dead wood, and inside logs. Centipedes are among the largest terrestrial invertebrate predators and often contribute significantly to the invertebrate predatory biomass in terrestrial ecosystems.

Description

Centipedes have a rounded or flattened head, bearing a pair of antennae at the forward margin. They have a pair of elongated mandibles, and two pairs of maxillae. The first pair of maxillae form the lower lip, and bear short palps. The first pair of limbs stretch forward from the body to cover the remainder of the mouth. These limbs, or maxillipeds, end in sharp claws and include venom glands that help the animal to kill or paralyse its prey.

Centipedes possess a variable number of ocelli, which are sometimes clustered together to form true compound eyes. Even so, it appears that centipedes are only capable of discerning light and dark, and not of true vision. Indeed, many species lack eyes altogether. In some species the final pair of legs act as sense organs similar to antennae, but facing backwards. An unusual sense organ found in some groups are the organs of Tömösvary. These are located at the base of the antennae, and consist of a disc-like structure with a central pore surrounded by sensory cells. They are probably used for sensing vibrations, and may even provide a sense of hearing.

Underside of *Scolopendra cingulata*, showing the forcipules

Forcipules are a unique feature found only in centipedes and in no other arthropods. The forcipules are modifications of the first pair of legs, forming a pincer-like appendage always found just behind the head. Forcipules are not true mouthparts, although they are used in the capture of prey items, injecting venom and holding onto captured prey. Venom glands run through a tube almost to the tip of each forcipule.

Behind the head, the body consists of fifteen or more segments. Most of the segments bear a single pair of legs, with the maxillipeds projecting forward from the first body segment, and the final two segments being small and legless. Each pair of legs is slightly longer than the pair immediately in front of it, ensuring that they do not overlap, and therefore reducing the chance that they will collide with each other while moving swiftly.

In extreme cases, the last pair of legs may be twice the length of the first pair. The final segment bears a telson and includes the openings of the reproductive organs.

Centipedes are predators, and mainly use their antennae to seek out their prey. The digestive tract forms a simple tube, with digestive glands attached to the mouthparts. Like insects, centipedes breathe through a tracheal system, typically with a single opening, or spiracle on each body segment. They excrete waste through a single pair of malpighian tubules.

Scolopendra gigantea, also known as the **Amazonian giant centipede**, is the largest existing species of centipede in the world, reaching over 30 cm (12 in) in length. It is known to eat lizards, frogs, birds, mice, and even bats, catching them in midflight, as well as rodents and spiders. The now extinct *Euphoberia* was the largest centipede, growing up to 1 m (39 in) in length.

Life cycle

A centipede protecting her eggmass

Centipede reproduction does not involve copulation. Males deposit a spermatophore for the female to take up. In one clade, this spermatophore is deposited in a web, and the male undertakes a courtship dance to encourage the female to engulf his sperm. In other cases, the males just leave them for the females to find. In temperate areas egg laying occurs in spring and summer but in subtropical and tropical areas there appears to be little seasonality to centipede breeding. It is also notable that there are a few known species of parthenogenetic centipedes.

The Lithobiomorpha, and Scutigeromorpha lay their eggs singly in holes in the soil, the female fills the hole in on the egg and leaves it. The number of eggs laid ranges from about 10 to 50. Time of development of the embryo to hatching is highly variable and may take from one to a few months. Time of development to reproductive period is highly variable within and among species. For example, it can take 3 years for *S. coleoptera* to achieve adulthood, whereas under the right conditions Lithiobiomorph species may reach a reproductive period in 1 year. In addition, centipedes are relatively long-lived when compared to their insect cousins. For example: the European *Lithobius forficatus* can live for 5 or 6 years. The combination of a small number of eggs laid, long gestation period, and long time of development to reproduction has led authors to label Lithobiomorph centipedes as K-selected.

Females of Geophilomorpha and Scolopendromorpha show far more parental care, the eggs 15 to 60 in number are laid in a nest in the soil or in rotten wood, the female stays with the eggs, guarding and licking them to protect them from fungi. The female in some species stays with the young after they have hatched, guarding them until they are ready to leave. If disturbed the females tend to either abandon the eggs of their young or eat them; abandoned eggs tend to fall prey to fungi rapidly. Some species of Scolopendromorpha are matriphagic, meaning that the offspring eat their mother.

Little is known of the life history of Craterostigmomorpha.

Anamorphy vs. epimorphy

Centipedes grow their legs at different points in their development. In the primitive condition, exhibited by the L, Scutigeromorpha and Craterostigmomorpha, development is anamorphic. That is to say, more pairs of legs are grown between moults; for example, *Scutigera coleoptrata*, the American house centipede, hatches with only 4 pairs of legs and in successive moults has 5, 7, 9, 11, 15, 15, 15 and 15 before becoming a sexually mature adult. Life stages with fewer than 15 pairs of legs are called larval stadia (~5 stages). After the full complement of legs is achieved, the now post-larval stadia (~5 stages) develop gonopods, sensory pores, more antennal segments, and more ocelli. All mature Lithobiomorph centipedes have 15 leg-bearing segments.

The Craterostigmomorpha only have one phase of anamorphis, with embryos having 12 pairs, and moultees 15.

The clade Epimorpha, consisting of orders Geophilomorpha and Scolopendromorpha, derived epimorphy. Here, all pairs of legs are developed in the embryonic stages, offspring do not develop more legs between moults. It is this clade that contains the *longest* centipedes; the maximum number of thoracic segments may also vary intra-specifically, often on a geographical basis; in most cases, females bear more legs than males. The number of leg-bearing segments varies widely, from 15 to 191, but the developmental mode of their creation means that they are always added in pairs – hence the total number of pairs is always odd.

Ecology

A centipede being eaten by a European roller

Centipedes are a predominantly predatory taxon. They are known as generalist predators which means that they have adapted to eat a variety of different available prey items. Examination of centipede gut contents suggest that plant material is an unimportant part of their diet although centipedes have been observed to eat vegetable matter when starved during laboratory experiments.

Centipedes are also known to be nocturnal. Studies on centipede activity rhythms confirm this, although there are a few observations of centipedes active during the day and one species *Strigamia chinophila* that is diurnal. What centipedes actually eat is not well known because of their cryptic lifestyle and thorough mastication of food. Laboratory feeding trials support that they will feed as generalists, taking most anything that is soft-bodied and in a reasonable size range. It has been suggested that earthworms provide the bulk of diets for Geophilomorphs, since Geophilomorphs burrow through the soil and earthworm bodies would be easily pierced by their poison claws. Observations suggest that Geophilomorphs cannot subdue earthworms larger than themselves, and so smaller earthworms may be a substantial proportion of their diet. Scolopendromorphs, given their size, are able to feed on vertebrates as well as invertebrates. They have been observed eating reptiles, amphibians, small mammals, bats and birds. Collembola may provide a large proportion of Lithiobiomorph diet. Little is known about Scutigeromorph or Craterostigmomorph diets. All centipedes are potential intraguild predators. Centipedes and spiders may frequently prey on one another.

Centipedes are eaten by a great many vertebrates and invertebrates, such as mongooses, mice, salamanders, beetles and snakes. They form an important item of diet for many species and the staple diet of some such as the African ant *Amblyopone pluto*, which feeds solely on geophilomorph centipedes, and the South African Cape black-headed snake *Aparallactus capensis*.

Centipedes are found in moist microhabitats. Water relations are an important aspect of their ecology, since they lose water rapidly in dry conditions. Water loss is a result of centipedes lacking a waxy covering of their exoskeleton and excreting waste nitrogen as ammonia, which requires extra water. Centipedes deal with water loss through a variety of adaptations. Geophilomorphs lose water less rapidly than Lithobiomorphs even though they have a greater surface area to volume ratio. This may be explained by the fact that Geophilomorphs have a more heavily sclerotized pleural membrane. Spiracle shape, size and ability to constrict also have an influence on rate of water loss. In addition, it has been suggested that number and size of coxal pores may be variables affecting centipede water balance.

Centipedes live in many different habitat types; forest, savannah, prairie, and desert to name a few. Some Geophilomorphs are adapted to littoral habitats, where they feed on barnacles. Species of all orders excluding Craterostigmomorpha have adapted to caves. Centipede densities have been recorded as high as $600/m^2$ and biomass as high as $500\ mg/m^2$ wet weight. Small geophilomorphs attain highest densities, followed by small Lithobiomorphs. Large Lithobiomorphs attain densities of $20/m^2$. One study of scolopendromorphs records *Scolopendra morsitans* in a Nigerian savannah at a density of $0.16/m^2$ and a biomass of $140\ mg/m^2$ wet weight.

Hazards to humans

Some species of centipede can be hazardous to humans because of their bite. Although a bite to an adult human is usually very painful and may cause severe swelling, chills, fever, and weakness, it is unlikely to be fatal. Bites can be dangerous to small children and those with allergies to bee stings. The bite of larger centipedes can induce anaphylactic shock in such people. Smaller centipedes usually do not puncture human skin.

Evolution

The fossil record of centipedes extends back to 430 million years ago, during the Late Silurian. They belong to the subphylum Myriapoda which includes Diplopoda, Symphyla, and Pauropoda. The oldest known fossil land animal, *Pneumodesmus newmani*, is a myriapod. Being among the earliest terrestrial animals, centipedes were one of the first to fill a fundamental niche as ground level generalist predators in detrital food webs. Today, centipedes are abundant and exist in many harsh habitats.

Within the myriapods, centipedes are believed to be the first of the extant classes to branch from the last common ancestor. There are five orders of centipedes: Craterostigmomorpha, Geophilomorpha, Lithobiomorpha, Scolopendromorpha, and Scutigeromorpha. These orders are united into the clade Chilopoda by the following synapomorphies:

1. The first post-cephalic appendage is modified to poison claws.
2. The embryonic cuticle on second maxilliped has an egg tooth.
3. The trochanter–prefemur joint is fixed.
4. There is a spiral ridge on the nucleus of the spermatozoon.

Chilopoda is then split into two clades: the Notostigmomorpha including the Scutigeromorpha and the Pluerostigmomorpha including the other four orders. The main difference is that the Notostigmomorpha have their spiracles located mid-dorsally. It was previously believed that Chilopoda was split into Anamorpha (Lithobiomorpha and Scutigeromorpha) and Epimorpha (Geophilomorpha and Scolopendromorpha), based on developmental modes, with the relationship of Craterostigmomorpha being uncertain. Recent phylogenetic analyses using combined molecular and morphological characters supports the previous phylogeny. Epimorpha still exists as a monophyletic group within the Pleurostigmomorpha, but Anamorpha is paraphyletic.

Geophilomorph centipedes have bene used to argue for the developmental constraint of evolution: that the evolvability of a trait, the number of segments in the case of geophilomorph centipedes, was constrained by the mode of development. The geophilomorph centipedes have variable segment numbers within species, yet as with all centipedes they always have an odd number of pairs of legs. In this taxon, the number of segments range from 27 to 191 but is never an even number.

Orders and families

Representatives of centipede orders

Scutigera coleoptrata (Scutigeromorpha: Scutigeridae)

Lithobius forficatus (Lithobiomorpha: Lithobiidae)

Geophilus flavus (Geophilomorpha: Geophilidae)

Scutigeromorpha

The **Scutigeromorpha** are anamorphic, reaching 15 leg-bearing segments in length. They are very fast creatures, and able to withstand falling at great speed: they reach up to 15 body lengths per second when dropped, surviving the fall. They are the only centipede group to retain their original compound eyes, with which a crystalline layer analogous to that seen in chelicerates and insects can be observed. They also bear long and multi-segmented antennae. Adaptation to a burrowing lifestyle has led to the degeneration of compound eyes in other orders. This feature is of great use in phylogenetic analysis. The group is the sole extant representative of the Notostigmomorpha, defined by having a single spiracle opening at the posterior of each dorsal plate. The more derived groups bear a plurality of spiracular openings on their sides, and are termed the Pleurostigmomorpha. Some even have several unpaired spiracles that can be found along the mid-dorsal line and closer to their posterior section of tergites. There are three families: Psellioididae, Scutigeridae and Scutigerinidae.

Lithobiomorpha

The **Lithobiomorpha** represent the other main group of anamorphic centipedes; they also reach a mature length of 15 thoracic segments. This group has lost the compound eyes, and sometimes has no eyes altogether. Instead, its eyes have facets or groups of facets. Its spiracles are paired and can be found laterally. Every leg-bearing segment of this organism has a separate tergite. It also has relatively short antennae and legs. Two families are included, Henicopidae and Lithobiidae.

Craterostigmomorpha

The **Craterostigmomorpha** are the least diverse centipede clade, comprising only two extant species, both in the genus *Ceratostigmus*. Their geographic range is restricted to Tasmania and New Zealand. They have a distinct body plan; their anamorphosis comprises a single stage; they grow from 12 to 15 segments in their first moult. Their low diversity and intermediate position between the primitive Anamorphic centipedes and the derived Epimorpha has led to them being likened to the platypus. They represent the survivors of a once diverse clade. Maternal brooding unites Craterostigomomorpha with the Epimorpha into the clade Phylactometria. This trait is thought to be closely linked with the presence of sternal pores, which secrete sticky or noxious secretions, which mainly serve to repel predators and parasites. The presence of these pores on the Devonian *Devonobius* permits its inclusion in this clade, allowing its divergence to be dated to 375 (or more) million years ago.

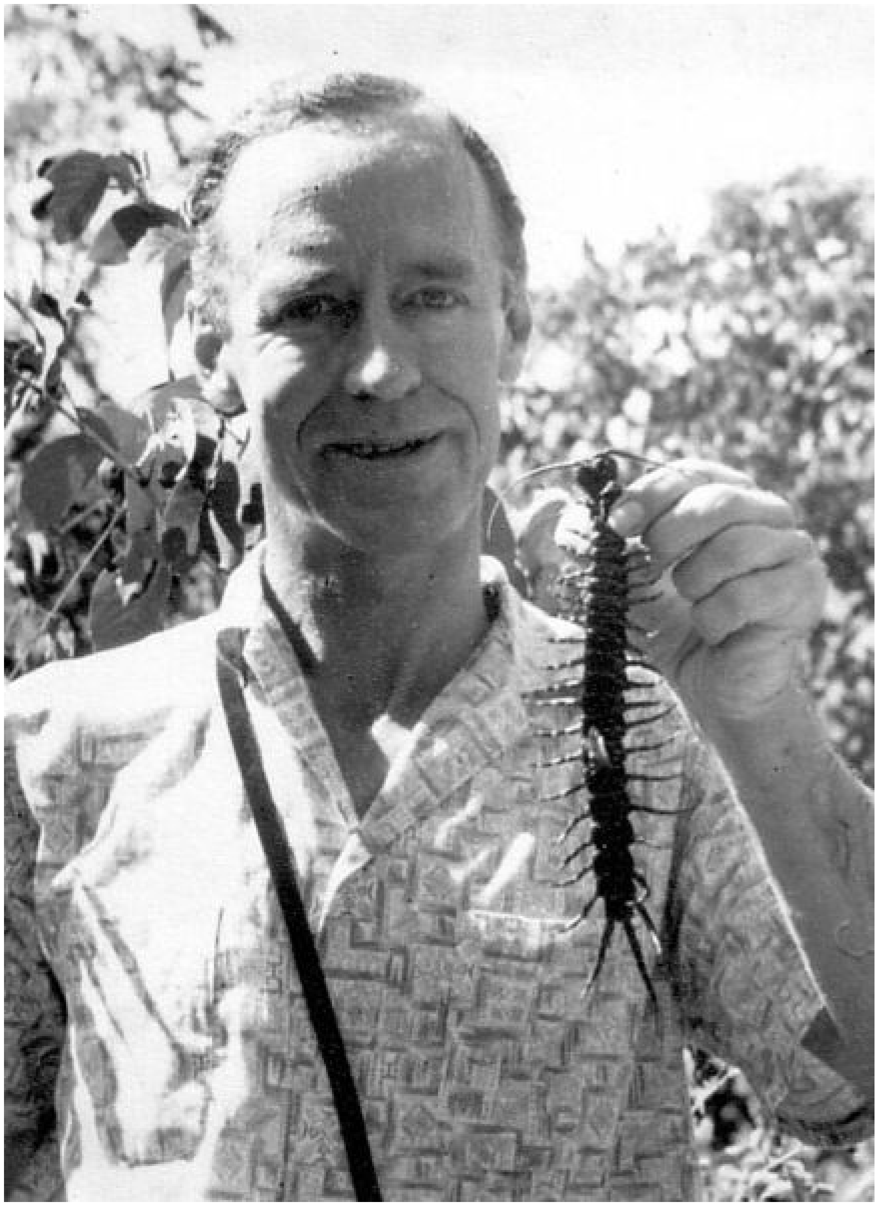
Scolopendromorpha

The **Scolopendromorpha** comprise 21 or more segments with the same number of paired legs. Their antennae have 17 or more segments. Their eyes have at least 4 facets on each side. The order comprises the three families Cryptopidae, Scolopendridae and Scolopocryptopidae.

Geophilomorpha

The Geophilomorpha bear upwards of 27 leg-bearing segments. They are eyeless and blind, and bear spiracles on all leg-bearing segments – in contrast to other groups, who only bear them on their 3rd, 5th, 8th, 10th and 12th segments – a "mid-body break", accompanied by a change in tagmatic shape, occurring roughly at the interchange from odd to even segments. This group, at 1260 spp. the most diverse, also contains the largest and leggiest specimens at 29 or more pairs of legs. They also have 14–segmented antennae. The group includes four families: Mecistocephalidae, Neogeophilidade, Geophilidae and Linotaeniidae.

Selected species



Man holding *Scolopendra gigantea*. Trinidad, 1961

Scientific name	Common name
Alipes grandidieri	Feather tail centipede
Ethmostigmus trigonopodus	Blue ring centipede
Lithobius forficatus	Stone centipede
Pachymerium ferrugineum	Earth centipede
Scolopendra galapagoensis	Galápagos centipede
Scolopendra gigantea	Peruvian giant orange leg centipede
Scolopendra heros	Giant red-headed centipede

Scolopendra morsitans	Red-headed centipede
Scolopendra polymorpha	Giant Sonoran centipede
Scolopendra subspinipes	Vietnamese centipede
Scutigera coleoptrata	House centipede

Chapter 9

Millipede

Millipede **Temporal range: 428–0 Ma** **Late Silurian to Recent**	
 Rusty millipede (*Trigoniulus corallinus*)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Myriapoda
Class:	**Diplopoda** De Blainville *in* Gervais, 1844

Millipedes are arthropods that have two pairs of legs per segment (except for the first segment behind the head which does not have any appendages at all, and the next few which only have one pair of legs). Each segment that has two pairs of legs is a result of two single segments fused together as one. Most millipedes have very elongated cylindrical bodies, although some are flattened dorso-ventrally, while pill millipedes are shorter and can roll into a ball, like a pillbug.

The name "millipede" is a compound word formed from the Latin roots *mille* ("thousand") and *pes* ("foot"). Despite their name, millipedes do not have 1,000 legs, although the rare species *Illacme plenipes* has up to 750. Common species have between

36 and 400 legs. The class contains around 10,000 species in 13 orders and 115 families. The giant African millipede (*Archispirostreptus gigas*), known as *shongololos*, is the largest species of millipede.

Millipedes are detritivores and slow moving. Most millipedes eat decaying leaves and other dead plant matter, moisturising the food with secretions and then scraping it in with its jaws. However, they can also be a minor garden pest, especially in greenhouses where they can cause severe damage to emergent seedlings. Signs of millipede damage include the stripping of the outer layers of a young plant stem and irregular damage to leaves and plant apices.

Millipedes can be easily distinguished from the somewhat similar and related centipedes (Class Chilopoda), which move rapidly, and have a single pair of legs for each body segment.

Evolution

This class of arthropod is thought to be among the first animals to have colonised land during the Silurian geologic period. These early forms probably ate mosses and primitive vascular plants. The oldest known land creature, *Pneumodesmus newmani*, was a 1 centimetre (0.39 in) long millipede, and lived 428 million years ago. In the Upper Carboniferous (340 to 280 million years ago), *Arthropleura* became the largest known land invertebrate of all time, reaching lengths of up to 2.6 metres (8 ft 6 in).

Characteristics

The North American millipede *Narceus americanus* — head with eyes

Millipedes range from 2 to 280 millimetres (0.079 to 11 in) in length, and can have as few as eleven, to over a hundred segments. They are generally black or brown in colour, although there are few brightly coloured species.

The millipede's most obvious feature is its large number of legs. Having very many short legs makes millipedes rather slow, but they are powerful burrowers. With their legs and body length moving in a wavelike pattern, they easily force their way underground head first. They also seem to have some engineering ability, reinforcing the tunnel by rearranging the particles around it. Their bodies have segmented sections which makes them move in a wave-like form.

The head of a millipede is typically rounded above and flattened below and bears large mandibles. The body is flattened or cylindrical, with a single chitinous plate above, one at each side, and two or three on the underside. In many millipedes, these plates are fused to varying degrees, sometimes forming a single cylindrical ring. The plates are typically hard, being impregnated with calcium salts.

Unlike centipedes and other similar animals, each segment bears two pairs of legs, rather than just one. This is because each is actually formed by the fusion of two embryonic segments, and is therefore properly referred to as a "diplosegment", or double segment.

The first few segments behind the head are not fused in this fashion, and the first segment is legless,called a **collum** segment while the second to fourth have one pair each. In some millipedes, the last few segments may also be legless. The final segment bears a telson.

Millipedes breathe through two pairs of spiracles on each diplosegment. Each opens into an internal pouch, and connects to a system of tracheae. The heart runs the entire length of the body, with an aorta stretching into the head. The excretory organs are two pairs of malpighian tubules, located near the mid-part of the gut.

The head contains a pair of sensory organs known as the Tömösváry organs. These are found just posterior and lateral to the antennae, and are shaped as small and oval rings at the base of the antennae. They are probably used to measure the humidity in the surroundings, and they may have some chemoreceptory abilities too. Millipede eyes consist of a number of simple flat lensed ocelli arranged in a group on the front/side of the head. Many species of millipedes, such as cave-dwelling millipedes, have secondarily lost their eyes.

According to Guinness World Records the African giant black millipede *Archispirostreptus gigas* can grow to 38.6 centimetres (15.2 in).

Diet

Most millipedes are herbivorous, and feed on decomposing vegetation or organic matter mixed with soil. A few species are omnivorous or carnivorous, and may prey on small arthropods, such as insects and centipedes, or on earthworms. Some species have piercing mouth parts that allow them to feed on plant juices.

The digestive tract is a simple tube with two pairs of salivary glands to help digest the food. Many millipedes moisten their food with saliva before eating it.

Reproduction

Epibolus pulchripes mating

Male millipedes can be differentiated from female millipedes by the presence of one or two pairs of legs modified into gonopods. These modified legs, which are usually on the seventh segment, are used to transfer sperm packets to the female during copulation. A few species are parthenogenetic, having few, if any, males.

The genital openings are located on the third segment, and are accompanied in the male by one or two penises, which deposit the sperm packets onto the gonopods. In the female, the genital pores open into a small chamber, or vulva, which is covered by a small hood-like cover, and is used to store the sperm after copulation.

Females lay between ten and three hundred eggs at a time, depending on species, fertilising them with the stored sperm as they do so. Many species simply deposit the eggs on moist soil or organic detritus, but some construct nests lined with dried faeces.

The young hatch after a few weeks, and typically have only three pairs of legs, followed by up to four legless segments. As they grow, they continually moult, adding further segments and legs as they do so. Some species moult within specially prepared chambers, which they may also use to wait out dry weather, and most species eat the shed exoskeleton after moulting. Millipedes live from one to ten years, depending on species.

Defense mechanisms

Due to their lack of speed and their inability to bite or sting, millipedes' primary defense mechanism is to curl into a tight coil — protecting their delicate legs inside an armored body exterior. Many species also emit poisonous liquid secretions or hydrogen cyanide gas through microscopic pores called **odoriferous glands** along the sides of their bodies as a secondary defense. Some of these substances are caustic and can burn the exoskeleton of ants and other insect predators, and the skin and eyes of larger predators. Animals such as Capuchin monkeys have been observed intentionally irritating millipedes in order to rub the chemicals on themselves to repel mosquitoes. At least one species, *Polyxenus fasciculatus* employs detachable bristles to entangle ants.

As far as humans are concerned, this chemical brew is fairly harmless, usually causing only minor effects on the skin, the main effect being discoloration, but other effects may also include pain, itching, local erythema, edema, blisters, eczema, and occasionally cracked skin. Eye exposures to these secretions causes general eye irritation and potentially more severe effects such as conjunctivitis and keratitis. First aid consists of flushing the area thoroughly with water; further treatment is aimed at relieving the local effects.

Classification

The living members of the Diplopoda are divided into fifteen orders in three subclasses. The basal subclass Penicillata contains 160 species whose exoskeleton is not calcified, and which are covered in setae or bristles. All other milipedes belong to the **Chilognatha** in the strict sense.

The subclass Pentazonia contains the short-bodied pill millipedes, which are capable of rolling themselves into a ball ("volvation"). The subclass Helminthomorpha contains the great majority of the species.

The subgroups of millipedes in phylogenetic sequence, from most basal to most advanced, are:

Glomeris marginata, a European pill millipede from the Order Glomerida

Harpaphe haydeniana, a species from the Order Polydesmida

Narceus americanus, an American species from the Order Spirobolida

- Basal genus *Eileticus* (fossil)
- Subclass Penicillata Latreille, 1831
    - Order Polyxenida Lucas, 1840
- Subclass Arthropleuridea (tentatively placed here; fossil)
- Subclass Zosterogrammida Wilson, 2005 (fossil)
- Subclass Pentazonia Brandt, 1833
    - Basal genus *Amynilyspes* (fossil)
    - Superorder Limacomorpha
        - Order Glomeridesmida Latzel, 1884
    - Superorder Oniscomorpha
        - Order Glomerida Leach, 1814
        - Order Sphaerotheriida Brandt, 1833
            - Family Sphaerotheriidae Koch, 1847
            - Family Sphaeropoeidae Brölemann, 1913
- Subclass Archipolypoda Scudder, 1882
- Subclass Helminthomorpha Pocock, 1887
    - Superorder Pleurojulida Schneider & Werneburg, 1998 (fossil)
    - Superorder Colobognatha (paraphyletic?)
        - Order Polyzoniida Gervais, 1844
        - Order Platydesmida DeSaussure, 1860

        - Order Siphonocryptida (formerly in Polyzoniida)
        - Order Siphonophorida Hoffman, 1980
    - Superorder "Merocheta"
        - Order Polydesmida Pocock, 1887
    - Superorder Nematophora
        - Basal genus *Hexecontasoma* (fossil)
        - Order Callipodida Bollman, 1893
        - Order Chordeumatida Koch, 1847
        - Order Stemmiulida Pocock, 1894
    - Superorder Diplocheta
        - Order "Xyloiuloida" Cook, 1895 (fossil)
        - Order Julida Brandt, 1833
        - Order Siphoniulida Cook, 1895
        - Order Spirobolida
        - Order Spirostreptida

Chapter 10

Insect

Insects Temporal range: 396–0 Ma Early Devonian – Recent	

Clockwise from top left: dancefly (*Empis livida*), long-nosed weevil (*Rhinotia hemistictus*), mole cricket (*Gryllotalpa brachyptera*), German wasp (*Vespula germanica*), emperor gum moth (*Opodiphthera eucalypti*), assassin bug (Harpactorinae)

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapoda
Class:	**Insecta** Linnaeus, 1758

Subclasses and classes
Monocondylia
Archaeognatha
Dicondylia
Pterygota

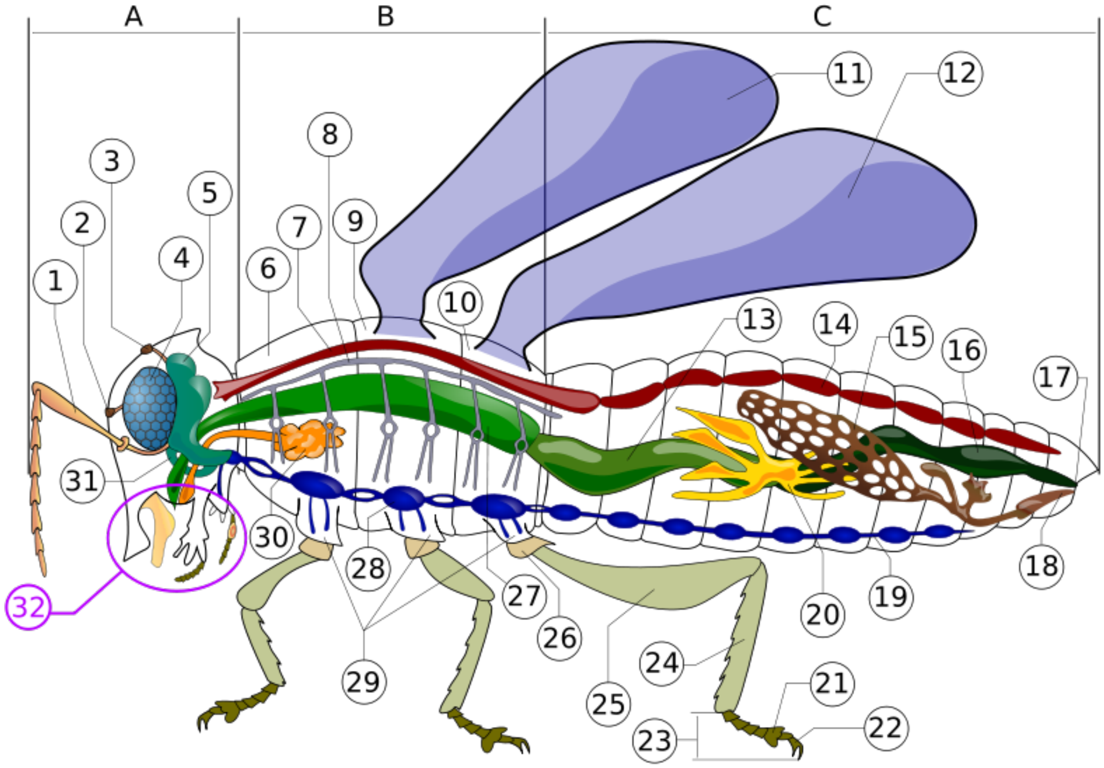
Insects (from Latin *insectum*, a calque of Greek ἔντομον [*éntomon*], "cut into sections") are a class within the arthropods that have a chitinous exoskeleton, a three-part body (head, thorax, and abdomen), three pairs of jointed legs, compound eyes, and two antennae. They are among the most diverse group of animals on the planet and include more than a million described species and represent more than half of all known living organisms. The number of extant species is estimated at between six and ten million, and potentially represent over 90% of the differing metazoan life forms on Earth. Insects may be found in nearly all environments, although only a small number of species occur in the oceans, a habitat dominated by another arthropod group, the crustaceans.

The life cycles of insects vary but most hatch from eggs. Insect growth is constrained by the inelastic exoskeleton and development involves a series of molts. The immature stages can differ from the adults in structure, habit and habitat and can include a passive pupal stage in those groups that undergo complete metamorphosis. Insects that undergo incomplete metamorphosis lack a pupal stage and adults develop through a series of nymphal stages. The higher level relationship of the hexapoda is unclear. Fossilized insects of enormous size have been found from the Paleozoic Era, including giant dragonflies with wingspans of 55 to 70 cm (22–28 in). The most diverse insect groups appear to have coevolved with flowering plants.

Insects typically move about by walking, flying or occasionally swimming. Because it allows for rapid yet stable movement, many insects adopt a tripedal gait in which they walk with their legs touching the ground in alternating triangles. Insects are the only invertebrates to have evolved flight. Many insects spend at least part of their life underwater, with larval adaptations that include gills and some adult insects are aquatic and have adaptations for swimming. Some species, like water striders, are capable of walking on the surface of water. Insects are mostly solitary, but some insects, such as certain bees, ants, and termites are social and live in large, well-organized colonies. Some insects, like earwigs, show maternal care, guarding their eggs and young. Insects can communicate with each other in a variety of ways. Male moths can sense the pheromones of female moths over distances of many kilometers. Other species communicate with sounds: crickets stridulate, or rub their wings together, to attract a mate and repel other males. Lampyridae in the beetle order Coleoptera communicate with light.

Humans regard certain insects as pests and attempt to control them using insecticides and a host of other techniques. Some insects damage crops by feeding on sap, leaves or fruits, a few bite humans and livestock, alive and dead, to feed on blood and some are capable of transmitting diseases to humans, pets and livestock. Many other insects are considered ecologically beneficial and a few provide direct economic benefit. Silkworms and bees have been domesticated by humans for the production of silk and honey, respectively.

External Morphology



Insect morphology

A- Head **B**- Thorax **C**- Abdomen

1. antenna
2. ocelli (lower)
3. ocelli (upper)
4. compound eye
5. brain (cerebral ganglia)
6. prothorax
7. dorsal blood vessel
8. tracheal tubes (trunk with spiracle)
9. mesothorax
10. metathorax
11. forewing
12. hindwing
13. mid-gut (stomach)
14. dorsal tube (Heart)
15. ovary
16. hind-gut (intestine, rectum & anus)
17. anus
18. oviduct
19. nerve chord (abdominal ganglia)
20. Malpighian tubes
21. tarsal pads

22. claws
23. tarsus
24. tibia
25. femur
26. trochanter
27. fore-gut (crop, gizzard)
28. thoracic ganglion
29. coxa
30. salivary gland
31. subesophageal ganglion
32. mouthparts

General body plan

Insects have segmented bodies supported by an exoskeleton, a hard outer covering made mostly of chitin. The segments of the body are organized into three distinctive but interconnected units, or tagmata: a head, a thorax, and an abdomen. The head supports a pair of sensory antennae, a pair of compound eyes, and, if present, one to three simple eyes (or ocelli) and three sets of variously modified appendages that form the mouthparts. The thorax has six segmented legs—one pair each for the prothorax, mesothorax and the metathorax segments making up the thorax—and, if present in the species, two or four wings. The abdomen consists of eleven segments, though in a few species of insects these segments may be fused together or reduced in size. The abdomen also contains most of the digestive, respiratory, excretory and reproductive internal structures.There is considerable variation and many adaptations in the body parts of insects especially wings, legs, antenna, mouth-parts etc.

Exoskeleton

Insect outer skeleton, the cuticle, is made up of two layers: the epicuticle, which is a thin and waxy water resistant outer layer and contains no chitin, and a lower layer called the procuticle. The procuticle is chitinous and much thicker than the epicuticle and has two layers: an outer layer known as the exocuticle and an inner layer known as the endocuticle. The tough and flexible endocuticle is built from numerous layers of fibrous chitin and proteins, criss-crossing each others in a sandwich pattern, while the exocuticle is rigid and hardened. The exocuticle is greatly reduced in many soft-bodied insects (e.g., caterpillars), especially during their larval stages.

Insects are the only invertebrates to have developed active flight capability, and this has played an important role in their success. These muscles are able to contract multiple times for each single nerve impulse, allowing the wings to beat faster than would ordinarily be possible. Having their muscles attached to their exoskeletons is more efficient and allows more muscle connections; crustaceans also use the same method, though all spiders use hydraulic pressure to extend their legs, a system inherited from their pre-arthropod ancestors. Unlike insects, though, most aquatic crustaceans are biomineralized with calcium carbonate extracted from the water.

Internal Morphology

Nervous system

The nervous system of an insect can be divided into a brain and a ventral nerve cord. The head capsule is made up of six fused segments, each with a pair of ganglia, or a cluster of nerve cells outside of the brain. The first three pairs of ganglia are fused into the brain, while the three following pairs are fused into a structure of three pairs of ganglia under the insect's esophagus, called the subesophageal ganglion.

The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction. Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. Some insects, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion.

At least a few insects have nociceptors, cells that detect and transmit sensations of pain. This was discovered in 2003 by studying the variation in reactions of larvae of the common fruitfly Drosophila to the touch of a heated probe and an unheated one. The larvae reacted to the touch of the heated probe with a stereotypical rolling behavior that was not exhibited when the larvae were touched by the unheated probe. Although nociception has been demonstrated in insects, there is not a consensus that insects feel pain consciously.

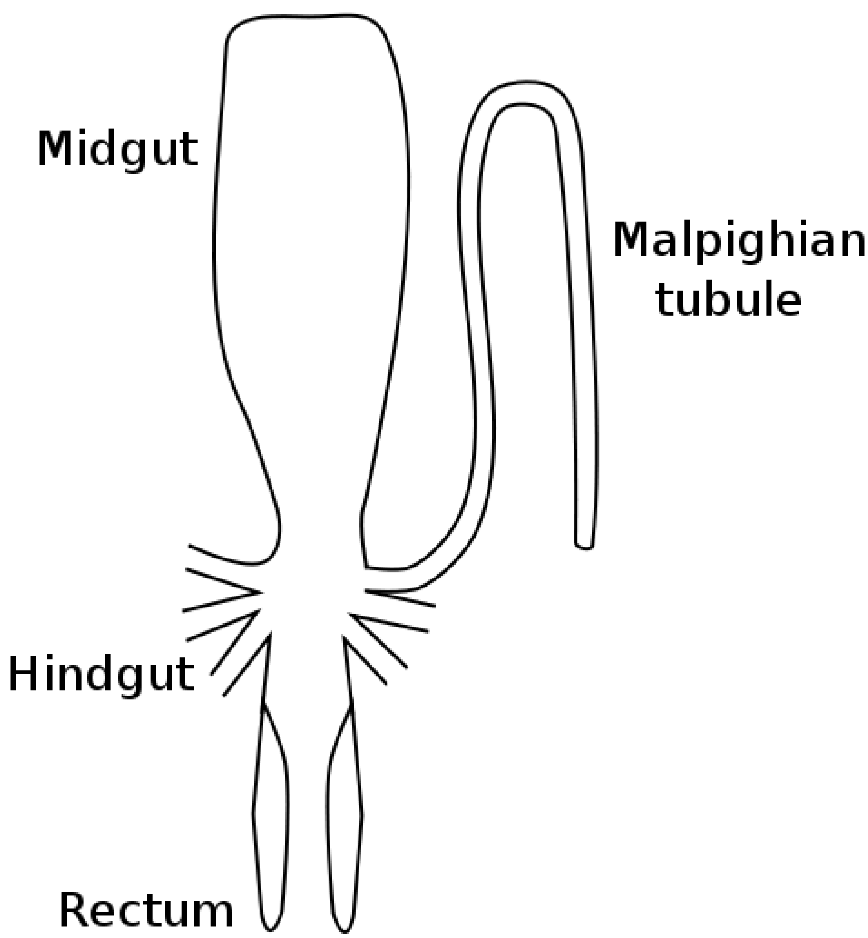
Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes. Most of this food is ingested in the form of macromolecules and other complex substances like proteins, polysaccharides, fats, and nucleic acids. These macromolecules must be broken down by catabolic reactions into smaller molecules like amino acids and simple sugars before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

The main structure of an insect's digestive system is a long enclosed tube called the alimentary canal, which runs lengthwise through the body. The alimentary canal directs food unidirectionally from the mouth to the anus. It has three sections, each of which performs a different process of digestion. In addition to the alimentary canal, insects also have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax, adjacent to the foregut.

The salivary glands (element 30 in numbered diagram) in an insect's mouth produce saliva. The salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium, located behind the hypopharynx. By moving its mouthparts (element 32 in numbered diagram) the insect can mix its food with saliva. The mixture of saliva and food then travels through the salivary tubes into the mouth, where it begins to break down. Some insects, like flies, have extra-oral digestion. Insects using extra-oral digestion expel digestive enzymes onto their food to break it down. This strategy allows insects to extract a significant proportion of the available nutrients from the food source. The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut



Stylized diagram of insect digestive tract showing malpighian tubule, from an insect of the order Orthoptera.

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is line with a cuticular lining made of chitin and proteins as protection from tough food. The foregut includes the buccal cavity (mouth), pharynx, esophagus, and Crop and proventriculus (any part may be highly modified) which both store food and signify when to continue passing onward to the midgut. Here, digestion starts as partially chewed food is broken down by saliva from the salivary glands. As the salivary glands produce fluid and carbohydrate-digesting enzymes (mostly amylases), strong muscles in the pharynx pump fluid into the buccal cavity, lubricating the food like the salivarium does, and helping blood feeders, and xylem and phloem feeders.

From there, the pharynx passes food to the esophagus, which could be just a simple tube passing it on to the crop and proventriculus, and then on ward to the midgut, as in most insects. Alternately, the foregut may expand into a very enlarged crop and proventriculus, or the crop could just be a diverticulum, or fluid filled structure, as in some Diptera species.

Bee defecating. Note the contraction of the anus which provides internal pressure.

Midgut

Once food leaves the crop, it passes to the midgut (element 13 in numbered diagram), also known as the mesenteron, where the majority of digestion takes place. Microscopic projections from the midgut wall, called microvilli, increase the surface area of the wall and allow more nutrients to be absorbed; they tend to be close to the origin of the midgut. In some insects, the role of the microvilli and where they are located may vary. For example, specialized microvilli producing digestive enzymes may more likely be near the end of the midgut, and absorption near the origin or beginning of the midgut.

Hindgut

In the hindgut (element 16 in numbered diagram), or proctodaeum, undigested food particles are joined by uric acid to form fecal pellets. The rectum absorbs 90% of the water in these fecal pellets, and the dry pellet is then eliminated through the anus (element 17), completing the process of digestion. The uric acid is formed using hemolymph waste products diffused from the Malpighian tubules (element 20). It is then emptied directly into the alimentary canal, at the junction between the midgut and hindgut. The number of Malpighian tubules possessed by a given insect varies between species, ranging from only two tubules in some insects to over 100 tubules in others.

Respiration and circulation

Insect respiration is accomplished without lungs. Instead, the insect respiratory system uses a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need it via their trachea (element 8 in numbered diagram). Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube which pulses peristaltically. Toward the thorax, the dorsal tube (element 14) divides into chambers and acts like the insect's heart. The opposite end of the dorsal tube is like the aorta of the insect circulating the hemolymph, arthropods' fluid analog of blood, inside the body cavity. Air is taken in through openings on the sides of the abdomen called spiracles.

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous and diffusive ventilation, to discontinuous gas exchange. During continuous gas exchange, oxygen is taken in and carbon dioxide is released in a continuous cycle. In discontinuous gas exchange, however, the insect takes in oxygen while it is active and small amounts of carbon dioxide are released when the insect is at rest. Diffusive ventilation is simply a form of continuous gas exchange that occurs by diffusion rather than physically taking in the oxygen. Some species of insect that are submerged also have adaptations to aid in respiration. As larvae, many insects have gills that can extract oxygen dissolved in water, while others need to rise to the water surface to replenish air supplies which may be held or trapped in special structures.

Reproduction and development

A pair of *Simosyrphus grandicornis* hoverflies mating in flight.

The majority of insects hatch from eggs. The fertilization and development takes place inside the egg, enclosed by a shell (chorion). Some species of insects, like the cockroach *Blaptica dubia*, as well as juvenile aphids and tsetse flies, are ovoviviparous. The eggs of ovoviviparous animals develop entirely inside the female, and then hatch immediately upon being laid. Some other species, such as those in the genus of cockroaches known as *Diploptera*, are viviparous, and thus gestate inside the mother and are born alive. Some insects, like parasitic wasps, show polyembryony, where a single fertilized egg divides into many and in some cases thousands of separate embryos.

The different forms of the male (top) and female (bottom) tussock moth *Orgyia recens* is an example of sexual dimorphism in insects.

Other developmental and reproductive variations include haplodiploidy, polymorphism, paedomorphosis or peramorphosis, sexual dimorphism, parthenogenesis and more rarely hermaphroditism. In haplodiploidy, which is a type of sex-determination system, the offspring's sex is determined by the number of sets of chromosomes an individual receives. This system is typical in bees and wasps. Polymorphism is the where a species may have different *morphs* or *forms*, as in the oblong winged katydid, which has four different varieties: green, pink, and yellow or tan. Some insects may retain phenotypes that are normally only seen in juveniles; this is called paedomorphosis. In peramorphosis, an opposite sort of phenomenon, insects take on previously unseen traits after they have matured into adults. Many insects display sexual dimorphism, in which males and females have notably different appearances, such as the moth *Orgyia recens* as an exemplar of sexual dimorphism in insects.

Some insects use parthenogenesis, a process in which the female can reproduce and give birth without having the eggs fertilized by a male. Many aphids undergo a form of parthenogenesis, called cyclical parthenogenesis, in which they alternate between one or many generations of asexual and sexual reproduction. In summer, aphids are generally female and parthenogenetic; in the autumn, males may be produced for sexual reproduction. Other insects produced by parthenogenesis are bees, wasps, and ants, in which they spawn males. However, overall, most individuals are female, which are produced by fertilization. The males are haploid and the females are diploid. More rarely, some insects display hermaphroditism, in which a given individual has both male and female reproductive organs.

Insect life-histories show adaptations to withstand cold and dry conditions. Some temperate region insects are capable of activity during winter, while some others migrate to a warmer climate or go into a state of torpor. Still other insects have evolved mechanisms of diapause that allow eggs or pupae to survive these conditions.

Metamorphosis

Metamorphosis in insects is the biological process of development all insects must undergo. There are two forms of metamorphosis: incomplete metamorphosis and complete metamorphosis.

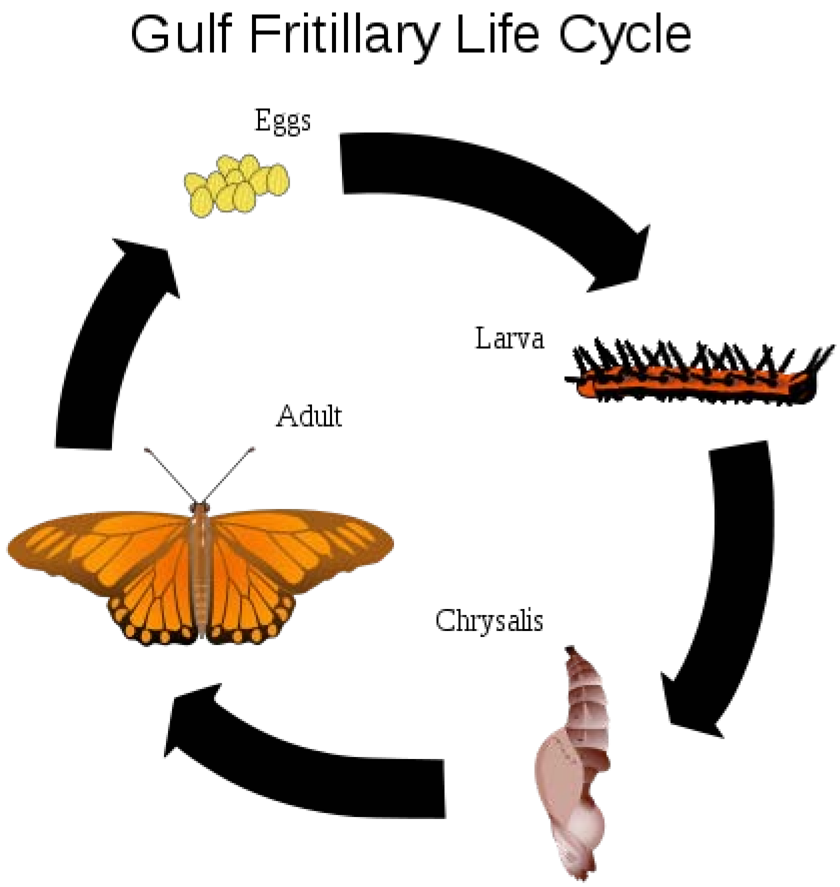
Incomplete metamorphosis

Insects that show hemimetabolism, or incomplete metamorphosis, change gradually by undergoing a series of molts. An insect molts when it outgrows its exoskeleton, which does not stretch and would otherwise restrict the insect's growth. The molting process begins as the insect's epidermis secretes a new epicuticle. After this new epicuticle is secreted, the epidermis releases a mixture of enzymes that digests the endocuticle and thus detaches the old cuticle. When this stage is complete, the insect makes its body swell by taking in a large quantity of water or air, which makes the old cuticle split along predefined weaknesses where the old exocuticle was thinnest. Other arthropods have a much different process and only molt; though must accommodate for the difference in exoskeleton structure and make up with other enzymes.

Immature insects that go through incomplete metamorphosis are called nymphs or in the case of dragonflies and damselflies as naiads. Nymphs are similar in form to the adult except for the presence of wings, which are not developed until adulthood. With each molt, nymphs grow larger and become more similar in appearance to adult insects.

Like other insects that develop through incomplete metamorphosis, this Southern Hawker dragonfly molts its exoskeleton (shown above) several times during its pre-adult life.

Complete metamorphosis



Gulf Fritillary life cycle, an example of holometabolism.

Holometabolism, or complete metamorphosis, is where the insect changes all in four stages, an egg or embryo, a larva, a pupa, and the adult or imago. In these species, egg hatches to produce a larva, which is generally worm-like in form. This worm-like form can be one of several varieties: eruciform (caterpillar-like), scarabaeiform (grub-like), campodeiform (elongated, flattened, and active), elateriform (wireworm-like) or vermiform (maggot-like). The larva grows and eventually becomes a pupa, a stage marked by reduced movement and often sealed within a cocoon. There are three types of pupae: obtect, exarate or coarctate. Obtect pupae are compact, with the legs and other appendages enclosed. Exarate pupae have their legs and other appendages free and extended. Coarctate pupae develop inside the larval skin. Insects undergo considerable change in form during the pupal stage, and emerge as adults. Butterflies are a well known example of an insects that undergo complete metamorphosis, although most insects use this life cycle. Some insects have evolved this system to hypermetamorphosis.

Some of the oldest and most successful insect groups, such Endopterygota, use a system of complete metamorphosis.Strangely though, complete metamorphosis is unique to certain insect orders, like Diptera, Lepidoptera, and Hymenoptera, and no other arthropods undergo it, but incomplete metamorphosis.

Senses and communication

Many insects possess very sensitive and/or specialized organs of perception. Some insects such as bees can perceive ultraviolet wavelengths, or detect polarized light, while the antennae of male moths can detect the pheromones of female moths over distances of many kilometers. There is a pronounced tendency for there to be a trade-off between visual acuity and chemical or tactile acuity, such that most insects with well-developed eyes have reduced or simple antennae, and vice-versa. There are a variety of different mechanisms by which insects perceive sound, while the patterns are not universal, insects can generally hear sound if they can produce it. Different insect species can have varying hearing, though most insects can hear only a narrow range of frequencies related to the frequency of the sounds they can produce. Mosquitoes have been found to hear up to 2 MHz., and some grasshoppers can hear up to 50 MHz. Certain predatory and parasitic insects can detect the characteristic sounds made by their prey or hosts, respectively. For instance, some nocturnal moths can perceive the ultrasonic emissions of bats, which helps them avoid predation. Insects that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts.

Some insects display a rudimentary sense of numbers, such as the solitary wasps that prey upon a single species. The mother wasp lays her eggs in individual cells and provides each egg with a number of live caterpillars on which the young feed when hatched. Some species of wasp always provide five, others twelve, and others as high as twenty-four caterpillars per cell. The number of caterpillars is different among species, but always the same for each sex of larva. The male solitary wasp in the genus *Eumenes* is smaller than the female, so the mother of one species supplies him with only five caterpillars; the larger female receives ten caterpillars in her cell.

Light production and vision

Insects have compound eyes and two antennae.

A few insects, such as members of the families Poduridae and Onychiuridae (Collembola), Mycetophilidae (Diptera), and the beetle families Lampyridae, Phengodidae, Elateridae and Staphylinidae are bioluminescent. The most familiar group are the fireflies, beetles of the family Lampyridae. Some species are able to control this light generation to produce flashes. The function varies with some species using them to attract mates, while others use them to lure prey. Cave dwelling larvae of *Arachnocampa* (Mycetophilidae, Fungus gnats) glow to lure small flying insects into sticky strands of silk. Some fireflies of the genus *Photuris* mimic the flashing of female *Photinus* species to attract males of that species, which are then captured and devoured. The colors of emitted light vary from dull blue (*Orfelia fultoni*, Mycetophilidae) to the familiar greens and the rare reds (*Phrixothrix tiemanni*, Phengodidae).

Most insects, except some species of cave dwelling crickets, are able to perceive light and dark. Many species have acute vision capable of detecting minute movements. The eyes include simple eyes or ocelli as well as compound eyes of varying sizes. Many species are able to detect light in the infrared, ultraviolet and the visible light wavelengths. Color vision has been demonstrated in many species and phylogenetic analysis suggests that UV-green-blue trichromacy existed from at least the Devonian period between 416 and 359 million years ago.

Sound production and hearing

Insects were the earliest organisms to produce and sense sounds. Insects make sounds mostly by mechanical action of appendages. In grasshoppers and crickets, this is achieved by stridulation. Cicadas make the loudest sounds among the insects by producing and amplifying sounds with special modifications to their body and musculature. The African cicada *Brevisana brevis* has been measured at 106.7 decibels at a distance of 50 cm (20 in). Some insects, such as the hawk moths and Hedylid butterflies, can hear ultrasound and take evasive action when they sense that they have been detected by bats. Some moths produce ultrasonic clicks that were once thought to have a role in jamming bat echolocation. The ultrasonic clicks were subsequently found to be produced mostly by unpalatable moths to warn bats, just as warning colorations are used against predators that hunt by sight. Some otherwise palatable moths have evolved to mimic these calls.

Very low sounds are also produced in various species of Coleoptera, Hymenoptera, Lepidoptera, Mantodea, and Neuroptera. These low sounds are simply the sounds made by the insect's movement. Through microscopic stridulatory structures located on the insect's muscles and joints, the normal sounds of the insect moving are amplified and can be used to warn or communicate with other insects. Most sound-making insects also have tympanal organs that can perceive airborne sounds. Some species in Hemiptera, such as the corixids (water boatmen), are known to communicate via underwater sounds. Most insects are also able to sense vibrations transmitted through surfaces. For example, an insect is caught in a spider web and struggles to escape. The vibrations it produces are sensed by the spider, who is alerted to its presence. Through these vibrations, the spider can tell where on the web the insect is located, as well as how big it is.

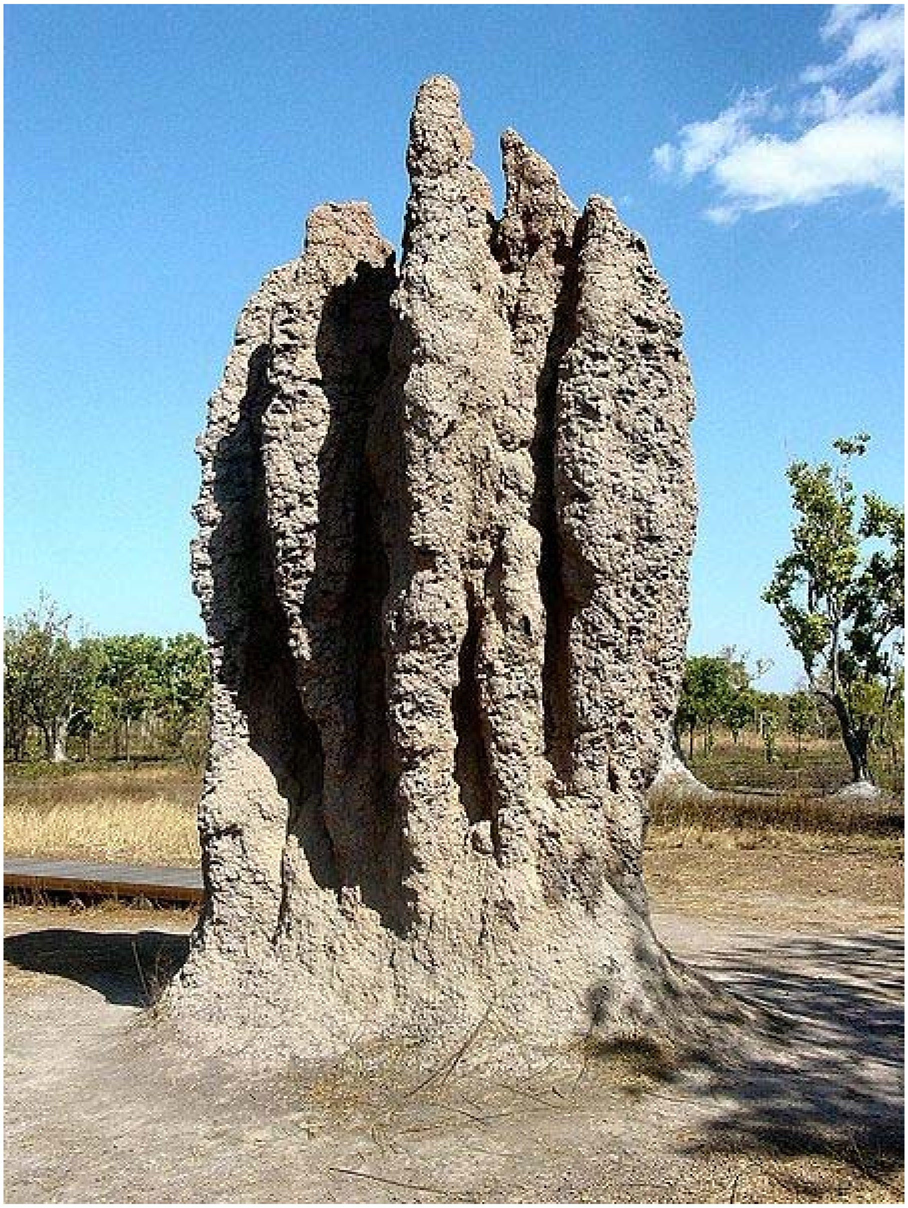
Communication using surface-borne vibrational signals is more widespread among insects because of size constraints in producing air-borne sounds. Insects cannot effectively produce low-frequency sounds, and high-frequency sounds tend to disperse more in a dense environment (such as foliage), so insects living in such environments communicate primarily using substrate-borne vibrations. The mechanisms of production of vibrational signals are just as diverse as those for producing sound in insects.

Some species use vibrations for communicating within members of the same species, such as to attract mates as in the songs of the shield bug *Nezara viridula*. Vibrations can also be used to communicate between entirely different species; lycaenid (gossamer-winged butterfly) caterpillars which are myrmecophilous (living in a mutualistic association with ants) communicate with ants in this way. The Madagascar hissing cockroach has the ability to press air through its spiracles to make a hissing noise as a sign of aggression; the Death's-head Hawkmoth makes a squeaking noise by forcing air out of their pharynx when agitated, which may also reduce aggressive worker honey bee behavior when the two are in close proximity.

Chemical communication

In addition to the use of sound for communication, a wide range of insects have evolved chemical means for communication. These chemicals, termed semiochemicals, are often derived from plant metabolites include those meant to attract, repel and provide other kinds of information. Pheromones, a type of semiochemical, are used for attracting mates of the opposite sex, for aggregating conspecific individuals of both sexes, for deterring other individuals from approaching, to mark a trail, and to trigger aggression in nearby individuals. Allomonea benefit their producer by the effect they have upon the receiver. Kairomones benefit their receiver instead of their producer. Synomones benefit the producer and the receiver. While some chemicals are targeted at individuals of the same species, others are used for communication across species. The use of scents is especially well known to have developed in social insects.

Social behavior



A cathedral mound created by termites (Isoptera).

Social insects, such as termites, ants and many bees and wasps, are the most familiar species of eusocial animal. They live together in large well-organized colonies that may be so tightly integrated and genetically similar that the colonies of some species are sometimes considered superorganisms. It is sometimes argued that the various species of honey bee are the only invertebrates (and indeed one of the few non-human groups) to have evolved a system of abstract symbolic communication where a behavior is used to *represent* and convey specific information about something in the environment. In this communication system, called dance language, the angle at which a bee dances represents a direction relative to the sun, and the length of the dance represents the distance to be flown.

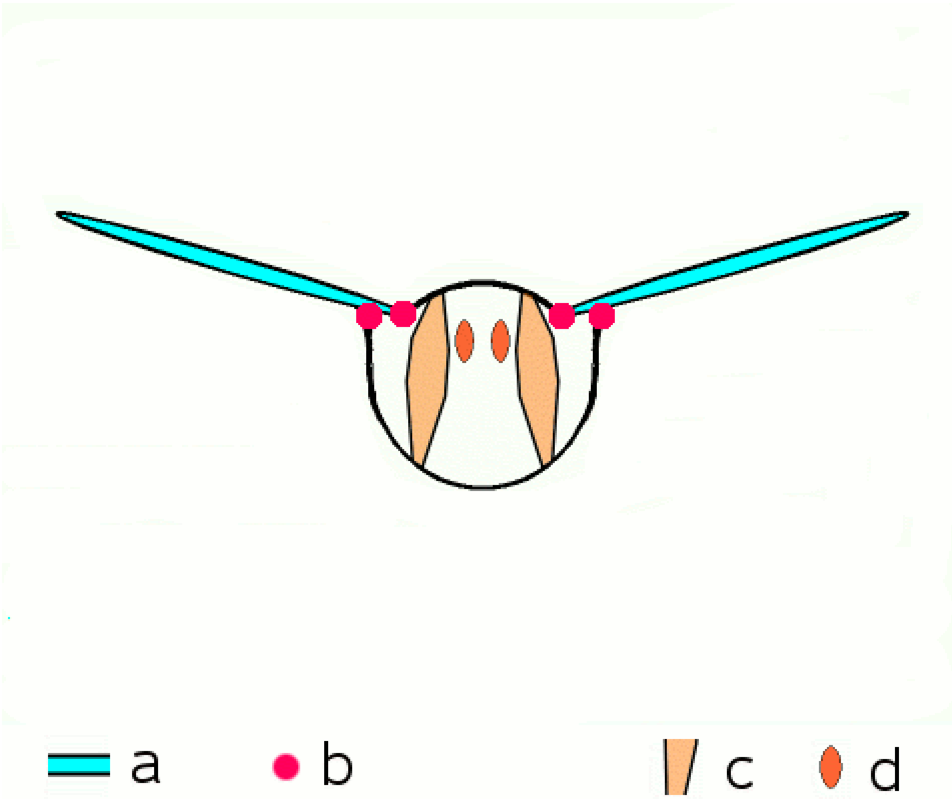
Only insects which live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to several kilometers' distance. In a phenomenon known as philopatry, insects that hibernate have shown the ability to recall a specific location up to a year after last viewing the area of interest. A few insects seasonally migrate large distances between different geographic regions (e.g., the overwintering areas of the Monarch butterfly).

Care of young

Most insects lead short lives as adults, and rarely interact with one another except to mate or compete for mates. A small number exhibit some form of parental care, where they will at least guard their eggs, and sometimes continue guarding their offspring until adulthood, and possibly even feeding them. Another simple form of parental care is to construct a nest (a burrow or an actual construction, either of which may be simple or complex), store provisions in it, and lay an egg upon those provisions. The adult does not contact the growing offspring, but it nonetheless does provide food. This sort of care is typical of bees and various types of wasps.

Locomotion

Flight



Basic motion of the insect wing in insect with an indirect flight mechanism scheme of dorsoventral cut through a thorax segment with
a wings
b joints
c dorsoventral muscles
d longitudinal muscles.

Insects are the only group of invertebrates to have developed flight. The evolution of insect wings has been a subject of debate. Some entomologists suggest that the wings are from paranotal lobes, or extensions from the insect's exoskeleton called the nota, called the *paranotal theory*. Other theories are based on a pleural origin. The pleuron is membrane on the sides of the thorax. These theories include suggestions that wings originated from modified gills, spiracular flaps or as from an appendage of the epicoxa. The *epicoxal theory* suggests the insect wings are modified epicoxal exites, a modified appendage at the base of the legs or coxa. In the Carboniferous age, some of the *Meganeura* dragonflies had as much as a 50 cm (20 in) wide wingspan. The appearance of gigantic insects has been found to be consistent with high atmospheric oxygen. The respiratory system of insects constrains their size, however the high oxygen in the atmosphere allowed larger sizes. The largest flying insects today are much smaller and include several moth species such as the Atlas moth and the White Witch (*Thysania* *agrippina*). Insect flight has been a topic of great interest in aerodynamics due partly to the inability of steady-state theories to explain the lift generated by the tiny wings of insects.

Unlike birds, many small insects are swept along by the prevailing winds although many of the larger insects are known to make migrations. Aphids are known to be transported long distances by low-level jet streams. As such, fine line patterns associated with converging winds within weather radar imagery, like the WSR-88D radar network, often represent large groups of insects.

Walking

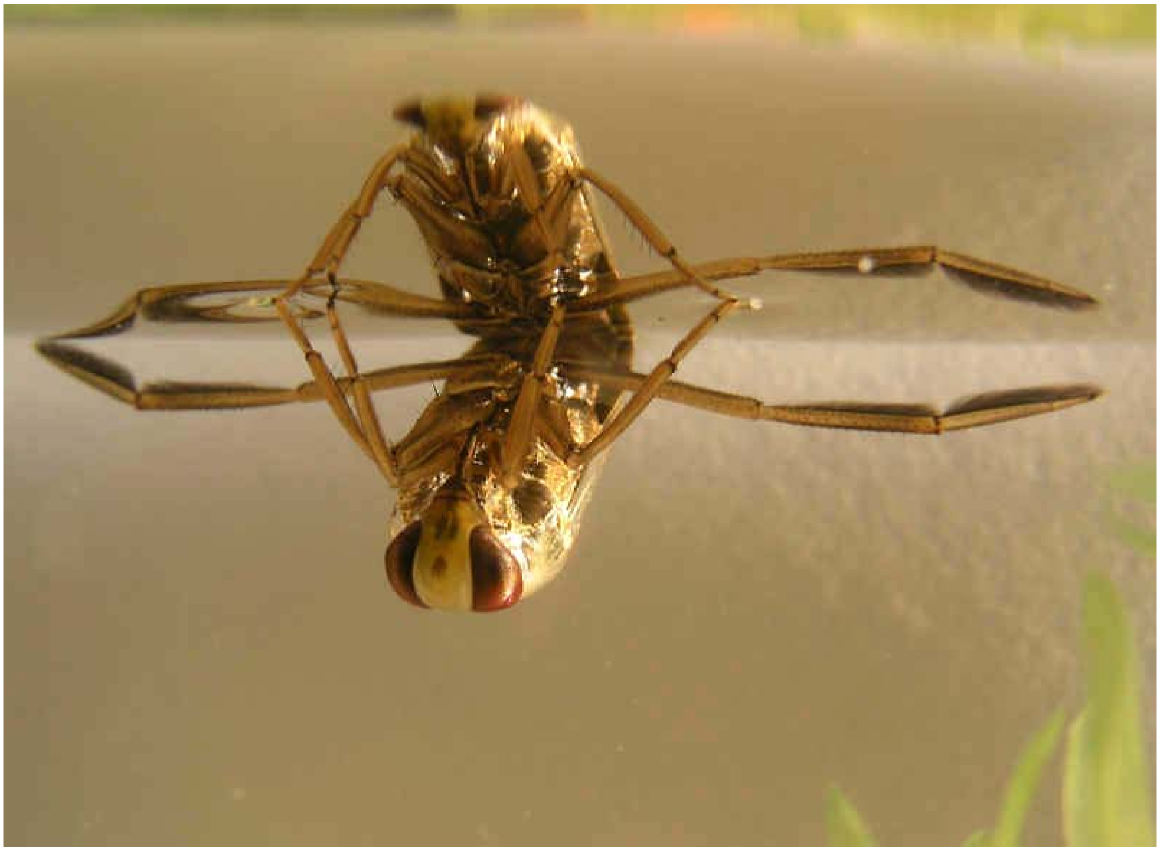
Many adult insects use six legs for walking and have adopted a tripedal gait. The tripedal gait allows for rapid walking while always having a stable stance and has been studied extensively in cockroaches. The legs are used in alternate triangles touching the ground. For the first step, the middle right leg and the front and rear left legs are in contact with the ground and move the insect forward, while the front and rear right leg and the middle left leg are lifted and moved forward to a new position. When they touch the ground to form a new stable triangle the other legs can be lifted and brought forward in turn and so on. The purest form of the tripedal gait is seen in insects moving at high speeds. However, this type of locomotion is not rigid and insects can adapt a variety of gaits. For example, when moving slowly, turning, or avoiding obstacles, four or more feet may be touching the ground. Insects can also adapt their gait to cope with the loss of one or more limbs.

Cockroaches are among the fastest insect runners and, at full speed, adopt a bipedal run to reach a high velocity in proportion to their body size. As cockroaches move very quickly, they need to be video recorded at several hundred frames per second to reveal their gait. More sedate locomotion is seen in the stick insects or walking sticks (Phasmatodea). A few insects have evolved to walk on the surface of the water, especially the bugs of the Gerridae family, commonly known as water striders. A few species of ocean-skaters in the genus *Halobates* even live on the surface of open oceans, a habitat that has few insect species.

Use in robotics

Insect walking is of particular interest as an alternative form of locomotion in robots. The study of insects and bipeds has a significant impact on possible robotic methods of transport. This may allow new robots to be designed that can traverse terrain that robots with wheels may be unable to handle.

Swimming



The backswimmer *Notonecta glauca* underwater, showing its paddle-like hindleg adaptation.

A large number of insects live either parts or the whole of their lives underwater. In many of the more primitive orders of insect, the immature stages are spent in an aquatic environment. Some groups of insects, like certain water beetles, have aquatic adults as well.

Many of these species have adaptations to help in under-water locomotion. Water beetles and water bugs have legs adapted into paddle-like structures. Dragonfly naiads use jet propulsion, forcibly expelling water out of their rectal chamber. Some species like the water striders are capable of walking on the surface of water. They can do this because their claws are not at the tips of the legs as in most insects, but recessed in a special groove further up the leg; this prevents the claws from piercing the water's surface film. Other insects such as the Rove beetle *Stenus* are known to emit pygidial gland secretions that reduce surface tension making it possible for them to move on the surface of water by Marangoni propulsion (also known by the German term *Entspannungsschwimmen*).

Phylogeny and systemics

Evolution has produced astonishing variety in insects. Pictured are some of the possible shapes of antennae.

The evolutionary relationships of insects to other animal groups remain unclear. Although more traditionally grouped with millipedes and centipedes, evidence has emerged favoring closer evolutionary ties with crustaceans. In the Pancrustacea theory, insects, together with Remipedia and Malacostraca, make up a natural clade. Other terrestrial arthropods, such as centipedes, millipedes, scorpions and spiders, are sometimes confused with insects since their body plans can appear similar, sharing (as do all arthropods) a jointed exoskeleton. However, upon closer examination their features differ significantly; most noticeably they do not have the six legs characteristic of adult insects.

The higher-level phylogeny of the arthropods continues to be a matter of debate and research. In 2008, researchers at Tufts University uncovered what they believe is the world's oldest known full-body impression of a primitive flying insect, a 300 million-year-old specimen from the Carboniferous Period. The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, from the 396 million year old Rhynie chert. It may have superficially resembled a modern-day silverfish insect. This species already possessed dicondylic mandibles (two articulations in the mandible), a feature associated with winged insects, suggesting that wings may already have evolved at this time. Thus, the first insects probably appeared earlier, in the Silurian period.

The origins of insect flight remain obscure, since the earliest winged insects currently known appear to have been capable fliers. Some extinct insects had an additional pair of winglets attaching to the first segment of the thorax, for a total of three pairs. As of 2009, there is no evidence that suggests that the insects were a particularly successful group of animals before they evolved to have wings.

Late Carboniferous and Early Permian insect orders include both extant groups and a number of Paleozoic species, now extinct. During this era, some giant dragonfly-like forms reached wingspans of 55 to 70 cm (22 to 28 in) making them far larger than any living insect. This gigantism may have been due to higher atmospheric oxygen levels that allowed increased respiratory efficiency relative to today. The lack of flying vertebrates could have been another factor. Most extinct orders of insects developed during the Permian period that began around 270 million years ago. Many of the early groups became extinct during the Permian-Triassic extinction event, the largest mass extinction in the history of the Earth, around 252 million years ago.

The remarkably successful Hymenopterans appeared as long as 146 million years ago in the Cretaceous period, but achieved their wide diversity more recently in the Cenozoic era, which began 66 million years ago. A number of highly successful insect groups evolved in conjunction with flowering plants, a powerful illustration of coevolution.

Many modern insect genera developed during the Cenozoic. Insects from this period on are often found preserved in amber, often in perfect condition. The body plan, or *morphology*, of such specimens is thus easily compared with modern species. The study of fossilized insects is called paleoentomology.

Evolutionary relationships

Insects are prey for a variety of organisms, including terrestrial vertebrates. The earliest vertebrates on land existed 400 million years ago and were large amphibious piscivores, through gradual evolutionary change, insectivory was the next diet type to evolve.

Insects were among the earliest terrestrial herbivores and acted as major selection agents on plants. Plants evolved chemical defenses against this herbivory and the insects in turn evolved mechanisms to deal with plant toxins. Many insects make use of these toxins to protect themselves from their predators. Such insects often advertise their toxicity using warning colors. This successful evolutionary pattern has also been utilized by mimics. Over time, this has led to complex groups of coevolved species. Conversely, some interactions between plants and insects, like pollination, are beneficial to both organisms. Coevolution has led to the development of very specific mutualisms in such systems.

Taxonomy

Traditional morphology-based or appearance-based systematics has usually given Hexapoda the rank of superclass, and identified four groups within it: insects (Ectognatha), springtails (Collembola), Protura and Diplura, the latter three being grouped together as Entognatha on the basis of internalized mouth parts. Supraordinal relationships have undergone numerous changes with the advent of methods based on evolutionary history and genetic data. A recent theory is that Hexapoda is polyphyletic (where the last common ancestor was not a member of the group), with the entognath classes having separate evolutionary histories from Insecta. Many of the traditional appearance-based taxa have been shown to be paraphyletic, so rather than using ranks like subclass, superorder and infraorder, it has proved better to use monophyletic groupings (in which the last common ancestor is a member of the group). The following represents the best supported monophyletic groupings for the Insecta.

Insects can be divided into two groups historically treated as subclasses: wingless insects, known as Apterygota, and winged insects, known as Pterygota. The Apterygota consist of the primitively wingless order of the silverfish (Thysanura). Archaeognatha make up the Monocondylia based on the shape of their mandibles, while Thysanura and Pterygota are grouped together as Dicondylia. It is possible that the Thysanura themselves are not monophyletic, with the family Lepidotrichidae being a sister group to the Dicondylia (Pterygota and the remaining Thysanura).

Paleoptera and Neoptera are the winged orders of insects differentiated by the presence of hardened body parts called sclerites; also, in Neoptera, muscles that allow their wings to fold flatly over the abdomen. Neoptera can further be divided into incomplete metamorphosis-based (Polyneoptera and Paraneoptera) and complete metamorphosis-based groups. It has proved difficult to clarify the relationships between the orders in Polyneoptera because of constant new findings calling for revision of the taxa. For example, Paraneoptera has turned out to be more closely related to Endopterygota than to the rest of the Exopterygota. The recent molecular finding that the traditional louse orders Mallophaga and Anoplura are derived from within Psocoptera has led to the new taxon Psocodea. Phasmatodea and Embiidina have been suggested to form Eukinolabia. Mantodea, Blattodea and Isoptera are thought to form a monophyletic group termed Dictyoptera.

It is likely that Exopterygota is paraphyletic in regard to Endopterygota. Matters that have had a lot of controversy include Strepsiptera and Diptera grouped together as Halteria based on a reduction of one of the wing pairs – a position not well-supported in the entomological community. The Neuropterida are often lumped or split on the whims of the taxonomist. Fleas are now thought to be closely related to boreid mecopterans. Many questions remain to be answered when it comes to basal relationships amongst endopterygote orders, particularly Hymenoptera.

The study of the classification or taxonomy of any insect is called systematic entomology. If one works with a more specific order or even a family, the term may also be made specific to that order or family, for example systematic dipterology.

Relationship to humans

Aedes aegypti, a parasite, and vector of dengue fever and yellow fever.

Many insects are considered pests by humans. Insects commonly regarded as pests include those that are parasitic (mosquitoes, lice, bed bugs), transmit diseases (mosquitoes, flies), damage structures (termites), or destroy agricultural goods (locusts, weevils). Many entomologists are involved in various forms of pest control, as in research for companies to produce insecticides, but increasingly relying on methods of biological pest control, or biocontrol. Biocontrol uses one organism to reduce the population density of another organism — the pest — and is considered a key element of integrated pest management.

Despite the large amount of effort focused at controlling insects, human attempts to kill pests with insecticides can backfire. If used carelessly the poison can kill all kinds of organisms in the area, including insects' natural predators such as birds, mice, and other insectivores. The effects of DDT's use exemplifies how some insecticides can threaten wildlife beyond intended populations of pest insects.

Because they help flowering plants to cross-pollinate, some insects are critical to agriculture. This European honey bee is gathering nectar while pollen collects on its body.

Although pest insects attract the most attention, many insects are beneficial to the environment and to humans. Some insects, like wasps, bees, butterflies, and ants, pollinate flowering plants. Pollination is a mutualistic relationship between plants and insects. As insects gather nectar from different plants of the same species, they also spread pollen from plants on which they have previously fed. This greatly increases plants' ability to cross-pollinate, which maintains and possibly even improves their evolutionary fitness. This ultimately affects humans since ensuring healthy crops is critical to agriculture. A serious environmental problem is the decline of populations of pollinator insects, and a number of species of insects are now cultured primarily for pollination management in order to have sufficient pollinators in the field, orchard or greenhouse at bloom time. Insects also produce useful substances such as honey, wax, lacquer and silk. Honey bees have been cultured by humans for thousands of years for honey, although contracting for crop pollination is becoming more significant for beekeepers. The silkworm has greatly affected human history, as silk-driven trade established relationships between China and the rest of the world.

The common fruitfly *Drosophila melanogaster* is one of the most widely used organisms in biological research.

Insects play important roles in biological research. For example, because of its small size, short generation time and high fecundity, the common fruit fly *Drosophila melanogaster* is a model organism for studies in the genetics of higher eukaryotes. *D. melanogaster* has been an essential part of studies into principles like genetic linkage, interactions between genes, chromosomal genetics, development, behavior, and evolution. Because genetic systems are well conserved among eukaryotes, understanding basic cellular processes like DNA replication or transcription in fruit flies can help to understand those processes in other eukaryotes, including humans. The genome of *D. melanogaster* was sequenced in 2000, reflecting the organism's important role in biological research.

A robberfly with its prey, a hoverfly. Insectivorous relationships such as these help control insect populations.

Insectivorous insects, or insects which feed on other insects, are beneficial to humans because they eat insects that could cause damage to agriculture and human structures. For example, aphids feed on crops and cause problems for farmers, but ladybugs feed on aphids, and can be used as a means to get significantly reduce pest aphid populations. While birds are perhaps more visible predators of insects, insects themselves account for the vast majority of insect consumption. Without predators to keep them in check, insects can undergo almost unstoppable population explosions.

Many insects, especially beetles, are scavengers that feed on dead animals and fallen trees and thereby recycle biological materials into forms found useful by other organisms. Insects are responsible for much of the process by which topsoil is created. The ancient Egyptian religion considered dung beetles sacred, and represented them as beetle-shaped amulets, or scarabs. Dung beetles have been used in countries including Australia as an agent of biological pest control to reduce the populations of pestilent flies and parasitic worms. The Australian Dung Beetle Project successfully introduced 23 species of dung beetle, including *Onthophagus gazella* and *Euoniticellus intermedius* from South Africa and Europe. This resulting in a 90% reduction in bush flies as well as improved soil fertility and quality.

Insects are also used in medicine, for example fly larvae (maggots) were formerly used to treat wounds to prevent or stop gangrene, as they would only consume dead flesh. This treatment is finding modern usage in some hospitals. Adult insects, such as crickets, and insect larvae of various kinds are also commonly used as fishing bait.

Entomophagy

In some parts of the world, insects are used for human food, while being a taboo in other places. In some cultures, insects, especially deep-fried cicadas, are considered to be delicacies, while in other places they form part of the normal diet as they have a high protein content for their mass. In most first-world countries, however, entomophagy, or the consumption of insects, is taboo. There are proponents of developing this use to provide a major source of protein in human nutrition. Since it is impossible to entirely eliminate pest insects from the human food chain, insects are present in many foods, especially grains. Food safety laws in many countries do not prohibit insect parts in food, but rather limit the quantity. According to cultural materialist anthropologist Marvin Harris, the eating of insects is taboo in cultures that have other protein sources such as fish or livestock.

In culture

Scarab beetles held religious and cultural symbolism in Old Egypt, Greece and some shamanistic Old World cultures. The ancient Chinese regarded cicadas as symbols of rebirth or immortality. In Mesopotamian literature, the epic poem of Gilgamesh has allusions to Odonata which signify the impossibility of immortality. Amongst the Aborigines of Australia of the Arrernte language groups, honey ants and witchety grubs served as personal clan totems. In the case of the 'San' bush-men of the Kalahari, it is the praying mantis which holds much cultural significance including creation and zen-like patience in waiting.