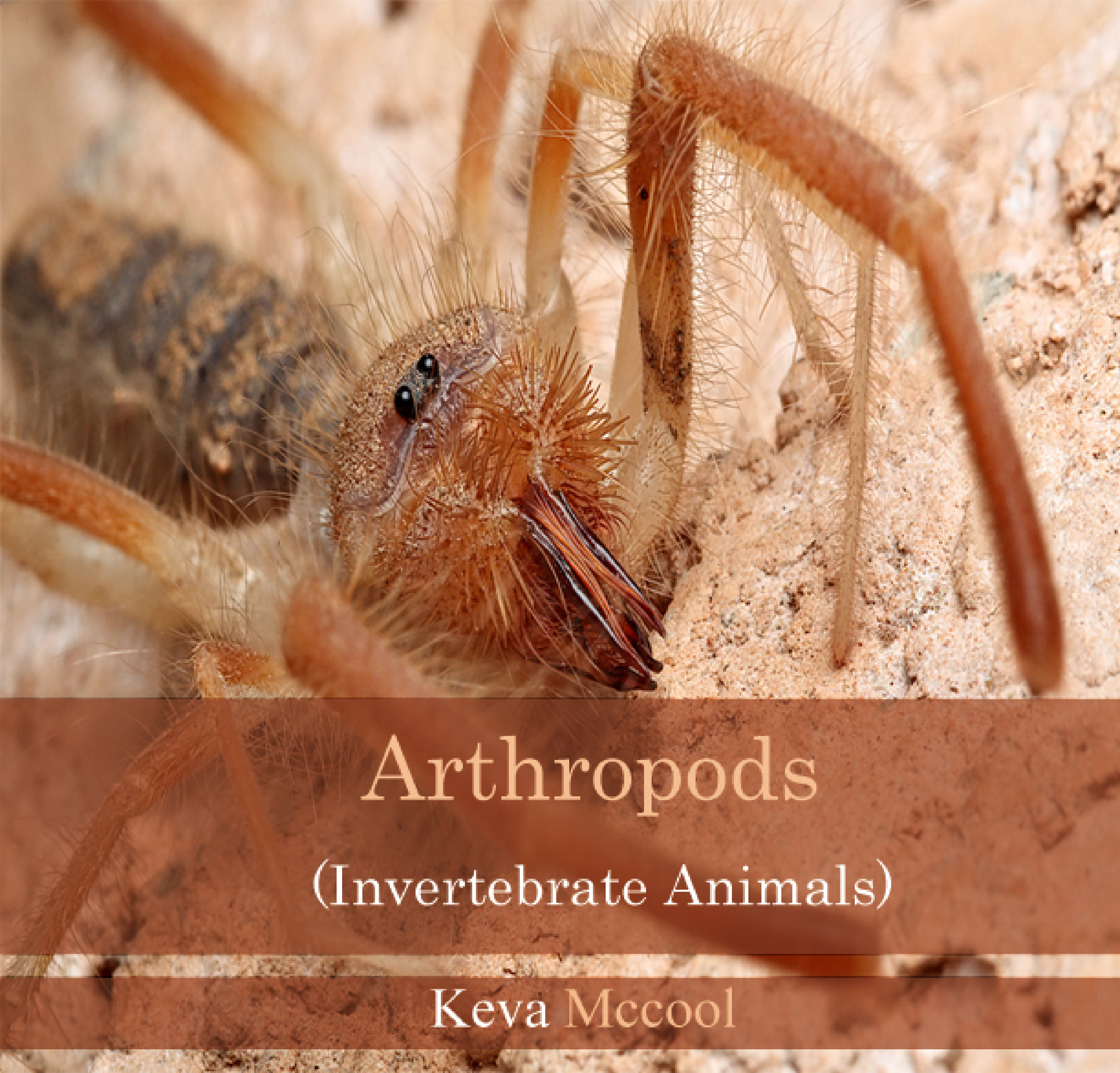

Arthropods

(Invertebrate Animals)

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Arthropod

Arthropod
Temporal range: 540–0 Ma
Cambrian – Recent

Extinct and modern arthropods

Scientific classification	
Domain:	Eukaryota
Kingdom:	Animalia
Subkingdom:	Eumetazoa
Superphylum:	Ecdysozoa
Phylum:	**Arthropoda** Latreille, 1829

Subphyla and Classes

- **Subphylum Trilobitomorpha**
    - Trilobita – trilobites (extinct)
- **Subphylum Chelicerata**
    - Arachnida – spiders, scorpions, etc.
    - Xiphosura – horseshoe crabs, etc.
    - Pycnogonida – sea spiders
    - Eurypterida – sea scorpions (extinct)
- **Subphylum Myriapoda**
    - Chilopoda – centipedes
    - Diplopoda – millipedes
    - Pauropoda
    - Symphyla
- **Subphylum Hexapoda**
    - Insecta – insects
    - Entognatha
- **Subphylum Crustacea**
    - Branchiopoda – brine shrimp etc.
    - Remipedia
    - Cephalocarida – horseshoe shrimp
    - Maxillopoda – barnacles, fish lice, etc.
    - Ostracoda – seed shrimp
    - Malacostraca – lobsters, crabs, shrimp, etc.

An **arthropod** is an invertebrate animal having an exoskeleton (external skeleton), a segmented body, and jointed appendages. Arthropods are members of the phylum **Arthropoda** (from Greek ἄρθρον *arthron*, "joint", and ποδός *podos* "foot", which together mean "jointed feet"), and include the insects, arachnids, crustaceans, and others. Arthropods are characterized by their jointed limbs and cuticles, which are mainly made of α-chitin; the cuticles of crustaceans are also biomineralized with calcium carbonate. The rigid cuticle inhibits growth, so arthropods replace it periodically by molting. The arthropod body plan consists of repeated segments, each with a pair of appendages. It is so versatile that they have been compared to Swiss Army knives, and it has enabled them to become the most species-rich members of all ecological guilds in most environments. They have over a million described species, making up more than 80% of all described living animal species, and are one of only two animal groups that are very successful in dry environments – the other being the amniotes. They range in size from microscopic plankton up to forms a few meters long.

Arthropods' primary internal cavity is a hemocoel, which accommodates their internal organs and through which their blood circulates; they have open circulatory systems. Like their exteriors, the internal organs of arthropods are generally built of repeated segments. Their nervous system is "ladder-like", with paired ventral nerve cords running through all segments and forming paired ganglia in each segment. Their heads are formed by fusion of varying numbers of segments, and their brains are formed by fusion of the ganglia of these segments and encircle the esophagus. The respiratory and excretory systems of arthropods vary, depending as much on their environment as on the subphylum to which they belong.

Their vision relies on various combinations of compound eyes and pigment-pit ocelli: in most species the ocelli can only detect the direction from which light is coming, and the compound eyes are the main source of information, but the main eyes of spiders are ocelli that can form images and, in a few cases, can swivel to track prey. Arthropods also have a wide range of chemical and mechanical sensors, mostly based on modifications of the many setae (bristles) that project through their cuticles.

Arthropods' methods of reproduction and development are diverse; all terrestrial species use internal fertilization, but this is often by indirect transfer of the sperm via an appendage or the ground, rather than by direct injection. Aquatic species use either internal or external fertilization. Almost all arthropods lay eggs, but scorpions give birth to live young after the eggs have hatched inside the mother. Arthropod hatchlings vary from miniature adults to grubs and caterpillars that lack jointed limbs and eventually undergo a total metamorphosis to produce the adult form. The level of maternal care for hatchlings varies from zero to the prolonged care provided by scorpions.

The versatility of the arthropod modular body plan has made it difficult for zoologists and paleontologists to classify them and work out their evolutionary ancestry, which dates back to the Cambrian period. From the late 1950s to late 1970s, it was thought that arthropods were polyphyletic, that is, there was no single arthropod ancestor. Now they are generally regarded as monophyletic. Historically, the closest evolutionary relatives of arthropods were considered to be annelid worms, as both groups have segmented bodies. This hypothesis is by now largely rejected, with annelids and molluscs forming the superphylum Lophotrochozoa. Many analyses support a placement of arthropods with cycloneuralians (or their constituent clades) in a superphylum Ecdysozoa. Overall however, the basal relationships of Metazoa are not yet well resolved. Likewise, the relationships between various arthropod groups are still actively debated.

Although arthropods contribute to human food supply both directly as food and more importantly as pollinators of crops, they also spread some of the most severe diseases and do considerable damage to livestock and crops.

Description

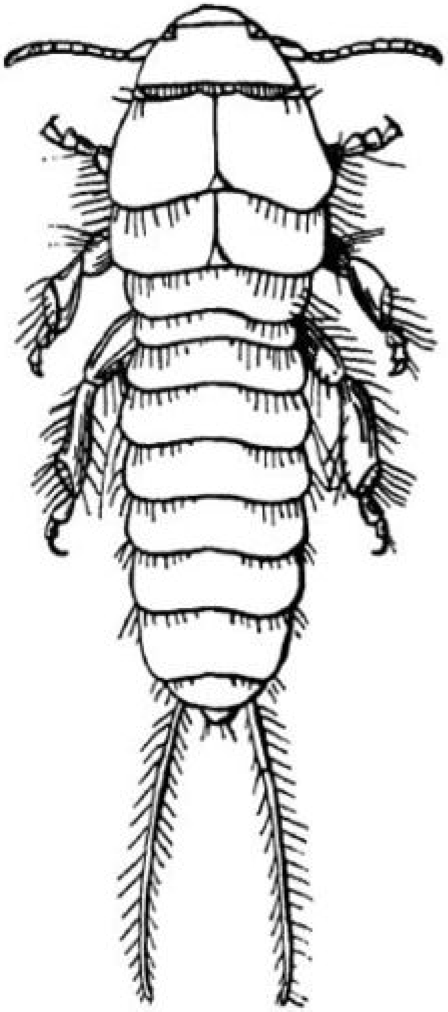
Arthropods are invertebrates with segmented bodies and jointed limbs. The limbs form part of an exoskeleton, which is mainly made of α-chitin, a derivative of glucose. One other group of animals, the tetrapods, has jointed limbs, but tetrapods are vertebrates and therefore have endoskeletons.

Diversity

One estimate indicates that arthropods have 1,170,000 described species, and account for over 80% of all known living animal species. Another study estimates that there are between 5 to 10 million extant arthropod species, both described and yet to be described. Estimating the total number of living species is extremely difficult because it often depends on a series of assumptions in order to scale up from counts at specific locations to estimates for the whole world. A study in 1992 estimated that there were 500,000 species of animals and plants in Costa Rica alone, of which 365,000 were arthropods.

They are important members of marine, freshwater, land and air ecosystems, and are one of only two major animal groups that have adapted to life in dry environments; the other is amniotes, whose living members are reptiles, birds and mammals. One arthropod subgroup, insects, is the most species-rich member of all ecological guilds (ways of making a living) in land and fresh-water environments. The lightest insects weigh less than 25 micrograms (millionths of a gram), while the heaviest weigh over 70 grams (2.5 oz). Some living crustaceans are much larger, for example the legs of the Japanese spider crab may span up to 4 metres (13 ft).

Segmentation



Hemimerus Hanseni.

(After Hansen.)

Segments and tagmata of an arthropod

The embryos of all arthropods are segmented, built from a series of repeated modules. The last common ancestor of living arthropods probably consisted of a series of undifferentiated segments, each with a pair of appendages that functioned as limbs. However all known living and fossil arthropods have grouped segments into tagmata in which segments and their limbs are specialized in various ways; The three-part appearance of many insect bodies and the two-part appearance of spiders is a result of this grouping; in fact there are no external signs of segmentation in mites. Arthropods also have two body elements that are not part of this serially repeated pattern of segments, an acron at the front, ahead of the mouth, and a telson at the rear, behind the anus. The eyes are mounted on the acron.

The original structure of arthropod appendages was probably biramous, with the upper branch acting as a gill while the lower branch was used for walking. In some segments of all known arthropods the appendages have been modified, for example to form gills, mouth-parts, antennae for collecting information, or claws for grasping; arthropods are "like Swiss Army knives, each equipped with a unique set of specialized tools." In many arthropods, appendages have vanished from some regions of the body, and it is particularly common for abdominal appendages to have disappeared or be highly modified.

The most conspicuous specialization of segments is in the head. The four major groups of arthropods – Chelicerata (includes spiders and scorpions), Crustacea (shrimps, lobsters, crabs, etc.), Tracheata (arthropods that breathe via channels into their bodies; includes insects and myriapods), and the extinct trilobites – have heads formed of various combinations of segments, with appendages that are missing or specialized in different ways. In addition some extinct arthropods, such as *Marrella*, belong to none of these groups, as their heads are formed by their own particular combinations of segments and specialized appendages. Working out the evolutionary stages by which all these different combinations could have appeared is so difficult that it has long been known as "the Arthropod head problem". In 1960 R.E. Snodgrass even hoped it would not be solved, as trying to work out solutions was so much fun.

Exoskeleton

Arthropod exoskeletons are made of cuticle, a non-cellular material secreted by the epidermis. Their cuticles vary in the details of their structure, but generally consist of three main layers: the epicuticle, a thin outer waxy coat that moisture-proofs the other layers and gives them some protection; the exocuticle, which consists of chitin and chemically hardened proteins; and the endocuticle, which consists of chitin and unhardened proteins. The exocuticle and endocuticle together are known as the procuticle. Each body segment and limb section is encased in hardened cuticle. The joints between body segments and between limb sections are covered by flexible cuticle.

The exoskeletons of most aquatic crustaceans are biomineralized with calcium carbonate extracted from the water. Some terrestrial crustaceans have developed means of storing the mineral, since on land they cannot rely on a steady supply of dissolved calcium carbonate. Biomineralization generally affects the exocuticle and the outer part of the endocuticle. Two recent hypotheses about the evolution of biomineralization in arthropods and other groups of animals propose that it provides tougher defensive armor, and that it allows animals to grow larger and stronger by providing more rigid skeletons; and in either case a mineral-organic composite exoskeleton is cheaper to build than an all-organic one of comparable strength.

The cuticle can have setae (bristles) growing from special cells in the epidermis. Setae are as varied in form and function as appendages. For example, they are often used as sensors to detect air or water currents, or contact with objects; aquatic arthropods use feather-like setae to increase the surface area of swimming appendages and to filter food particles out of water; aquatic insects, which are air-breathers, use thick felt-like coats of setae to trap air, extending the time they can spend under water; heavy, rigid setae serve as defensive spines.

Although all arthropods use muscles attached to the inside of the exoskeleton to flex their limbs, some still use hydraulic pressure to extend them, a system inherited from their pre-arthropod ancestors; for example, all spiders extend their legs hydraulically and can generate pressures up to eight times their resting level.

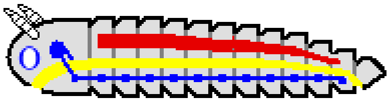
Molting

The exoskeleton cannot stretch and thus restricts growth. Arthropods therefore replace their exoskeletons by molting, or shedding the old exoskeleton after growing a new one that is not yet hardened. Molting cycles run nearly continuously until an arthropod reaches full size.

In the initial phase of molting, the animal stops feeding and its epidermis releases molting fluid, a mixture of enzymes that digests the endocuticle and thus detaches the old cuticle. This phase begins when the epidermis has secreted a new epicuticle to protect it from the enzymes, and the epidermis secretes the new exocuticle while the old cuticle is detaching. When this stage is complete, the animal makes its body swell by taking in a large quantity of water or air, and this makes the old cuticle split along predefined weaknesses where the old exocuticle was thinnest. It commonly takes several minutes for the animal to struggle out of the old cuticle. At this point the new one is wrinkled and so soft that the animal cannot support itself and finds it very difficult to move, and the new endocuticle has not yet formed. The animal continues to pump itself up to stretch the new cuticle as much as possible, then hardens the new exocuticle and eliminates the excess air or water. By the end of this phase the new endocuticle has formed. Many arthropods then eat the discarded cuticle to reclaim its materials.

Because arthropods are unprotected and nearly immobilized until the new cuticle has hardened, they are in danger both of being trapped in the old cuticle and of being attacked by predators. Molting may be responsible for 80 to 90% of all arthropod deaths.

Internal organs



🟥 = heart
🟨 = gut
🟦 = brain, nerve cord, ganglia

O = eye

Basic arthropod body structure

Arthropod bodies are also segmented internally, and the nervous, muscular, circulatory and excretory systems have repeated components. Arthopods come from a lineage of animals that have a coelom, a membrane-lined cavity between the gut and the body wall that accommodates the internal organs. The strong, segmented limbs of arthropods eliminate the need for one of the coelom's main ancestral functions, as a hydrostatic skeleton, which muscles compress in order to change the animal's shape and thus enable it to move. Hence the coelom of the arthropod is reduced to small areas around the reproductive and excretory systems. Its place is largely taken by a hemocoel, a cavity that runs most of the length of the body and through which blood flows.

Arthropods have open circulatory systems, although most have a few short, open-ended arteries. In chelicerates and crustaceans, the blood carries oxygen to the tissues, while hexapods use a separate system of tracheae. Many crustaceans, but few chelicerates and tracheates, use respiratory pigments to assist oxygen transport. The most common respiratory pigment in arthropods is copper-based hemocyanin; this is used by many crustaceans and a few centipedes. A few crustaceans and insects use iron-based hemoglobin, the respiratory pigment used by vertebrates. As with other invertebrates and unlike among vertebrates, the respiratory pigments of those arthropods that have them are generally dissolved in the blood and rarely enclosed in corpuscles.

The heart is typically a muscular tube that runs just under the back and for most of the length of the hemocoel. It contracts in ripples that run from rear to front, pushing blood forwards. Elastic ligaments, or small muscles, connect the heart to the body wall and expand sections that are not being squeezed by the heart muscle. Along the heart run a series of paired ostia, non-return valves that allow blood to enter the heart but prevent it from leaving before it reaches the front.

Arthropods have a wide variety of respiratory systems. Small species often do not have any, since their high ratio of surface area to volume enables simple diffusion through the body surface to supply enough oxygen. Crustacea usually have gills that are modified appendages. Many arachnids have book lungs. Tracheae, systems of branching tunnels that run from the openings in the body walls, deliver oxygen directly to individual cells in many insects, myriapods and arachnids.

Living arthropods have paired main nerve cords running along their bodies below the gut, and in each segment the cords form a pair of ganglia from which sensory and motor nerves run to other parts of the segment. Although the pairs of ganglia in each segment often appear physically fused, they are connected by commissures (relatively large bundles of nerves), which give arthropod nervous systems a characteristic "ladder-like" appearance. The brain is in the head, encircling and mainly *above* the esophagus. It consists of the fused ganglia of the acron and one or two of the foremost segments that form the head – a total of three pairs of ganglia in most arthropods, but only two in chelicerates, which do not have antennae or the ganglion connected to them. The ganglia of other head segments are often close to the brain and function as part of it. In insects these other head ganglia combine into a pair of subesophageal ganglia, under and behind the esophagus. Spiders take this process a step further, as *all* the segmental ganglia are incorporated into the subesophageal ganglia, which occupy most of the space in the cephalothorax (front "super-segment").

There are two different types of arthropod excretory systems. In aquatic arthropods, the end-product of biochemical reactions that metabolise nitrogen is ammonia, which is so toxic that it needs to be diluted as much as possible with water. The ammonia is then eliminated via any permeable membrane, mainly through the gills. All crustaceans use this system, and its high consumption of water may be responsible for the relative lack of success of crustaceans as land animals. Various groups of terrestrial arthropods have independently developed a different system: the end-product of nitrogen metabolism is uric acid, which can be excreted as dry material; Malpighian tubules filter the uric acid and other nitrogenous waste out of the blood in the hemocoel, and dump these materials into the hindgut, from which they are expelled as feces. Most aquatic arthropods and some terrestrial ones also have organs called nephridia ("little kidneys"), which extract other wastes for excretion as urine.

Senses

The stiff cuticles of arthropods 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, arthropods have modified their cuticles into elaborate arrays of sensors. Various touch sensors, mostly 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. Pressure sensors often take the form of membranes that function as eardrums, but are connected directly to nerves rather than to auditory ossicles. The antennae of most hexapods include sensor packages that monitor humidity, moisture and temperature.

Head of a wasp with three ocelli (centre), and compound eyes at the left and right

Most arthropods have sophisticated visual systems that include one or more usually both of compound eyes and pigment-cup ocelli ("little eyes"). In most cases ocelli are only capable of detecting the direction from which light is coming, using the shadow cast by the walls of the cup. However the main eyes of spiders are pigment-cup ocelli that are capable of forming images, and those of jumping spiders can rotate to track prey.

Compound eyes consist of fifteen to several thousand independent ommatidia, columns that are usually hexagonal in cross section. Each ommatidium is an independent sensor, with its own light-sensitive cells and often with its own lens and cornea. Compound eyes have a wide field of view, and can detect fast movement and, in some cases, the polarization of light. On the other hand the relatively large size of ommatidia makes the images rather coarse, and compound eyes are shorter-sighted than those of birds and mammals – although this is not a severe disadvantage, as objects and events within 20 centimetres (7.9 in) are most important to most arthropods. Several arthropods have color vision, and that of some insects has been studied in detail; for example, the ommatidia of bees contain receptors for both green and ultra-violet.

Most arthropods lack balance and acceleration sensors, and rely on their eyes to tell them which way is up. The self-righting behavior of cockroaches is triggered when pressure sensors on the underside of the feet report no pressure. However many malacostracan crustaceans have statocysts, which provide the same sort of information as the balance and motion sensors of the vertebrate inner ear.

The proprioceptors of arthropods, sensors that report the force exerted by muscles and the degree of bending in the body and joints, are well understood. However, little is known about what other internal sensors arthropods may have.

Reproduction and development

Compsobuthus werneri female with young (white)

A few arthropods, such as barnacles, are hermaphroditic, that is, each can have the organs of both sexes. However, individuals of most species remain of one sex all their lives. A few species of insects and crustaceans can reproduce by parthenogenesis, for example, without mating, especially if conditions favor a "population explosion". However most arthropods rely on sexual reproduction, and parthenogenetic species often revert to sexual reproduction when conditions become less favorable. Aquatic arthropods may breed by external fertilization, as for example frogs also do, or by internal fertilization, where the ova remain in the female's body and the sperm must somehow be inserted. All known terrestrial arthropods use internal fertilization, as unprotected sperm and ova would not survive long in these environments. In a few cases the sperm transfer is direct from the male's penis to the female's oviduct, but it is more often indirect. Some crustaceans and spiders use modified appendages to transfer the sperm to the female. On the other hand, many male terrestrial arthropods produce spermatophores, waterproof packets of sperm, which the females take into their bodies. A few such species rely on females to find spermatophores that have already been deposited on the ground, but in most cases males only deposit spermatophores when complex courtship rituals look likely to be successful.

The nauplius larva of a prawn

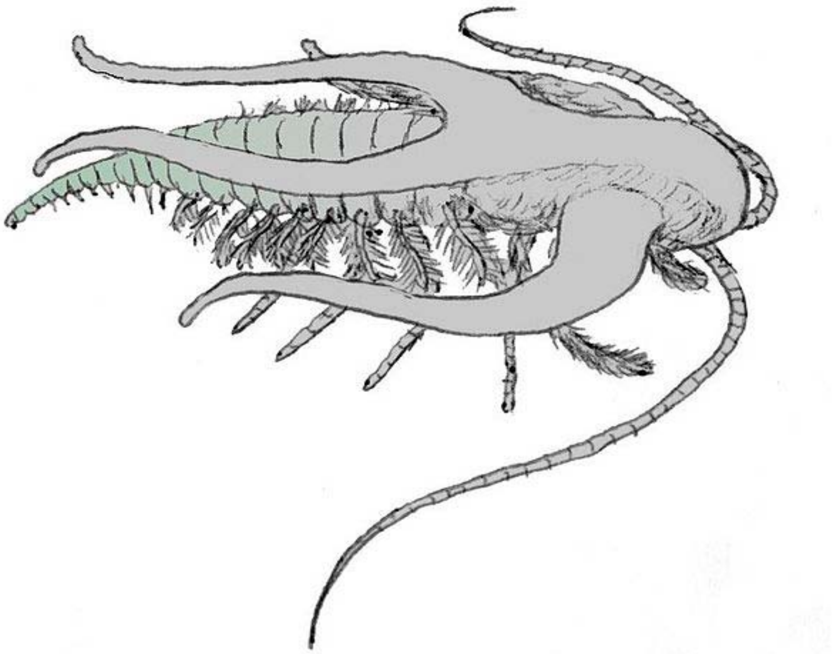
Most arthropods lay eggs, but scorpions are viviparous: they produce live young after the eggs have hatched inside the mother, and are noted for prolonged maternal care. Newly born arthropods have diverse forms, and insects alone cover the range of extremes. Some hatch as apparently miniature adults (direct development), and in some cases, such as silverfish, the hatchlings do not feed and may be helpless until after their first molt. Many insects hatch as grubs or caterpillars, which do not have segmented limbs or hardened cuticles, and metamorphose into adult forms by entering an inactive phase in which the larval tissues are broken down and re-used to build the adult body. Dragonfly larvae have the typical cuticles and jointed limbs of arthropods but are flightless water-breathers with extendable jaws. Crustaceans commonly hatch as tiny nauplius larvae that have only three segments and pairs of appendages.

Evolution

Last common ancestor

The last common ancestor of all arthropods is reconstructed as a modular organism with each module covered by its own sclerite (armor plate) and bearing a pair of biramous limbs. Whether the ancestral limb was uniramous or biramous is far from a settled debate, though. This Ur-arthropod had a ventral mouth, pre-oral antennae and dorsal eyes at the front of the body. It was a non-discriminatory sediment feeder, processing whatever sediment came its way for food.

Fossil record



Marrella, one of the puzzling arthropods from the Burgess Shale

It has been proposed that the Ediacaran animals *Parvancorina* and *Spriggina*, from around 555 Mya, were arthropods. Small arthropods with bivalve-like shells have been found in Early Cambrian fossil beds dating 541 to 539 million years ago in China. The earliest Cambrian trilobite fossils are about 530 million years old, but the class was already quite diverse and worldwide, suggesting that they had been around for quite some time. Re-examination in the 1970s of the Burgess Shale fossils from about 505 million years ago identified many arthropods, some of which could not be assigned to any of the well-known groups, and thus intensified the debate about the Cambrian explosion. A fossil of *Marrella* from the Burgess Shale has provided the earliest clear evidence of molting.

The earliest fossil crustaceans date from about 513 million years ago in the Cambrian, and fossil shrimp from about 500 million years ago apparently formed a tight-knit procession across the seabed. Crustacean fossils are common from the Ordovician period onwards. They have remained almost entirely aquatic, possibly because they never developed excretory systems that conserve water.

Arthropods provide the earliest identifiable fossils of land animals, from about 419 million years ago in the Late Silurian, and terrestrial tracks from about 450 million years ago appear to have been made by arthropods. Arthropods were well pre-adapted to colonize land, because their existing jointed exoskeletons provided protection against desiccation, support against gravity and a means of locomotion that was not dependent on water. Around the same time the aquatic, scorpion-like eurypterids became the largest ever arthropods, some as long as 2.5 metres (8.2 ft).

The oldest known arachnid is the trigonotarbid *Palaeotarbus jerami*, from about 420 million years ago in the Silurian period. *Attercopus fimbriunguis*, from 386 million years ago in the Devonian period, bears the earliest known silk-producing spigots, but its lack of spinnerets means it was not one of the true spiders, which first appear in the Late Carboniferous over 299 million years ago. The Jurassic and Cretaceous periods provide a large number of fossil spiders, including representatives of many modern families. Fossils of aquatic scorpions with gills appear in the Silurian and Devonian periods, and the earliest fossil of an air-breathing scorpion with book lungs dates from the Early Carboniferous period.

The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, dated at 396 to 407 million years ago, but its mandibles are of a type found only in winged insects, which suggests that the earliest insects appeared in the Silurian period. The Mazon Creek lagerstätten from the Late Carboniferous, about 300 million years ago, include about 200 species, some gigantic by modern standards, and indicate that insects had occupied their main modern ecological niches as herbivores, detritivores and insectivores. Social termites and ants first appear in the Early Cretaceous, and advanced social bees have been found in Late Cretaceous rocks but did not become abundant until the Mid Cenozoic.

Evolutionary family tree

The velvet worm (Onychophora) is closely related to arthropods

From the late 1950s to the late 1970s, Sidnie Manton and others argued that arthropods are polyphyletic, in other words, they do not share a common ancestor *that was itself an arthropod*. Instead, they proposed that three separate groups of "arthropods" evolved separately from common worm-like ancestors: the chelicerates, including spiders and scorpions; the crustaceans; and the uniramia, consisting of onychophorans, myriapods and hexapods. These arguments usually bypassed trilobites, as the evolutionary relationships of this class were unclear. Proponents of polyphyly argued the following: that the similarities between these groups are the results of convergent evolution, as natural consequences of having rigid, segmented exoskeletons; that the three groups use different chemical means of hardening the cuticle; that there were significant differences in the construction of their compound eyes; that it is hard to see how such different configurations of segments and appendages in the head could have evolved from the same ancestor; and that crustaceans have biramous limbs with separate gill and leg branches, while the other two groups have uniramous limbs in which the single branch serves as a leg.

Further analysis and discoveries in the 1990s reversed this view, and led to acceptance that arthropods are monophyletic, in other words they do share a common ancestor *that was itself an arthropod*. For example Graham Budd's analyses of *Kerygmachela* in 1993 and of *Opabinia* in 1996 convinced him that these animals were similar to onychophorans and to various Early Cambrian "lobopods", and he presented an "evolutionary family tree" that showed these as "aunts" and "cousins" of all arthropods. These changes made the scope of the term "arthropod" unclear, and Claus Nielsen proposed that the wider group should be labelled "Panarthropoda" ("all the arthropods") while the animals with jointed limbs and hardened cuticles should be called "Euarthropoda" ("true arthropods").

A contrary view was presented in 2003, when Jan Bergström and Xian-Guang Hou argued that, if arthropods were a "sister-group" to any of the anomalocarids, they must have lost and then re-evolved features that were well-developed in the anomalocarids. The earliest known arthropods ate mud in order to extract food particles from it, and possessed variable numbers of segments with unspecialized appendages that functioned as both gills and legs. Anomalocarids were, by the standards of the time, huge and sophisticated predators with specialized mouths and grasping appendages, fixed numbers of segments some of which were specialized, tail fins, and gills that were very different from those of arthropods. This reasoning implies that *Parapeytoia*, which has legs and a backward-pointing mouth like that of the earliest arthropods, is a more credible closest relative of arthropods than is *Anomalocaris*. In 2006, they suggested that arthropods were more closely related to lobopods and tardigrades than to anomalocarids.

Higher up the "family tree", the Annelida have traditionally been considered the closest relatives of the Panarthropoda, since both groups have segmented bodies, and the combination of these groups was labelled Articulata. There had been competing proposals that arthropods were closely related to other groups such as nematodes, priapulids and tardigrades, but these remained minority views because it was difficult to specify in detail the relationships between these groups.

In the 1990s, molecular phylogenetic analyses of DNA sequences produced a coherent scheme showing arthropods as members of a superphylum labelled Ecdysozoa ("animals that molt"), which contained nematodes, priapulids and tardigrades but excluded annelids. This was backed up by studies of the anatomy and development of these animals, which showed that many of the features that supported the Articulata hypothesis showed significant differences between annelids and the earliest Panarthropods in their details, and some were hardly present at all in arthropods. This hypothesis groups annelids with molluscs and brachiopods in another superphylum, Lophotrochozoa.

If the Ecdysozoa hypothesis is correct, then segmentation of arthropods and annelids either has evolved convergently or has been inherited from a much older ancestor and subsequently lost in several other lineages, such as the non-arthropod members of the Ecdysozoa.

Classification of arthropods

Euarthropods are typically classified into five subphyla, of which one is extinct:

1. **Trilobites** are a group of formerly numerous marine animals that disappeared in the Permian-Triassic extinction event, though they were in decline prior to this killing blow, having been reduced to one order in the Late Devonian extinction.
2. **Chelicerates** include spiders, mites, scorpions and related organisms. They are characterised by the presence of chelicerae, appendages just above / in front of the mouth. Chelicerae appear in scorpions as tiny claws that they use in feeding, but those of spiders have developed as fangs that inject venom.
3. **Myriapods** comprise millipedes, centipedes, and their relatives and have many body segments, each bearing one or two pairs of legs. They are sometimes grouped with the hexapods.
4. **Hexapods** comprise insects and three small orders of insect-like animals with six thoracic legs. They are sometimes grouped with the myriapods, in a group called Uniramia, though genetic evidence tends to support a closer relationship between hexapods and crustaceans.
5. **Crustaceans** are primarily aquatic (a notable exception being woodlice) and are characterised by having biramous appendages. They include lobsters, crabs, barnacles, crayfish, shrimp and many others.

Aside from these major groups, there are also a number of fossil forms, mostly from the Early Cambrian, which are difficult to place, either from lack of obvious affinity to any of the main groups or from clear affinity to several of them. *Marrella* was the first one to be recognized as significantly different from the well-known groups.

The phylogeny of the major extant arthropod groups has been an area of considerable interest and dispute. The most recent studies tend to suggest a paraphyletic Crustacea with different hexapod groups nested within it. Myriapoda is grouped with Chelicerata in some recent studies (forming Myriochelata), and with Pancrustacea in other studies (forming Mandibulata). The placement of the extinct trilobites is also a frequent subject of dispute.

Since the International Code of Zoological Nomenclature recognises no priority above the rank of family, many of the higher-level groups can be referred to by a variety of different names.

Interaction with humans

Insects and scorpions on sale in a food stall in Bangkok

Crustaceans such as crabs, lobsters, crayfish, shrimps and prawns have long been part of human cuisine, and are now farmed on a large commercial scale. Insects and their grubs are at least as nutritious as meat, and are eaten both raw and cooked in many non-European cultures. Cooked tarantulas are considered a delicacy in Cambodia, and by the Piaroa Indians of southern Venezuela, after the highly irritant hairs – the spider's main defense system – are removed. Humans also unintentionally eat arthropods in other foods, and food safety regulations lay down acceptable contamination levels for different kinds of food material. The intentional cultivation of arthropods and other small animal for human food, referred to as minilivestock, is now emerging in animal husbandry as an ecologically sound concept.

However, the greatest contribution of arthropods to human food supply is by pollination: a 2008 study examined the 100 crops that FAO lists as grown for food, and estimated pollination's economic value as €153 billion, or 9.5% of the value of world agricultural production used for human food in 2005. Besides pollinating, bees produce honey, which is the basis of a rapidly growing industry and international trade.

The red dye cochineal, produced from a Central American species of insect, was economically important to the Aztecs and Mayans, and while the region was under

Spanish control, becoming Mexico's second most-lucrative export; and it is now regaining some of the ground it lost to synthetic competitors. 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. Forensic entomology uses evidence provided by arthropods to establish the time and sometimes the place of death of a human, and in somes cases the cause.

The relative simplicity of the arthropods' body plan, allowing them to move on a variety of surfaces both on land and in water, have made them useful as models for robotics. The redundancy provided by segments allows arthropods and biomimetic robots to move normally even with damaged or lost appendages.

Diseases transmitted by insects

Disease	Insect	Cases per year	Deaths per year
Malaria	*Anopheles* mosquito	267 M	1 to 2 M
Yellow fever	*Aedes* mosquito	4,432	1,177
Filariasis	*Culex* mosquito	250 M	unknown

Although arthropods are the most numerous phylum on Earth, and thousands of arthropod species are venomous, they inflict relatively few serious bites and stings on humans. Far more serious are the effects on humans of diseases carried by blood-sucking insects. Other blood-sucking insects infect livestock with diseases that kill many animals and greatly reduce the usefulness of others. Ticks can cause tick paralysis and several parasite-borne diseases in humans. A few of the closely related mites also infest humans, causing intense itching, and others cause allergic diseases, including hay fever, asthma and eczema.

Many species of arthropods, principally insects but also mites, are agricultural and forest pests. The mite *Varroa destructor* has become the largest single problem faced by beekeepers worldwide. Efforts to control arthropod pests by large-scale use of pesticides have caused long term effects on human health and on biodiversity. Increasing arthropod resistance to pesticides has led to the development of integrated pest management using a wide range of meaures including biological control. Predatory mites may be useful in controlling some mite pests.

Chapter- 2

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	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapoda

Class:	**Insecta** Linnaeus, 1758

Subclasses

- Monocondylia (Archaeognatha)
- Dicondylia

Apterygota
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.

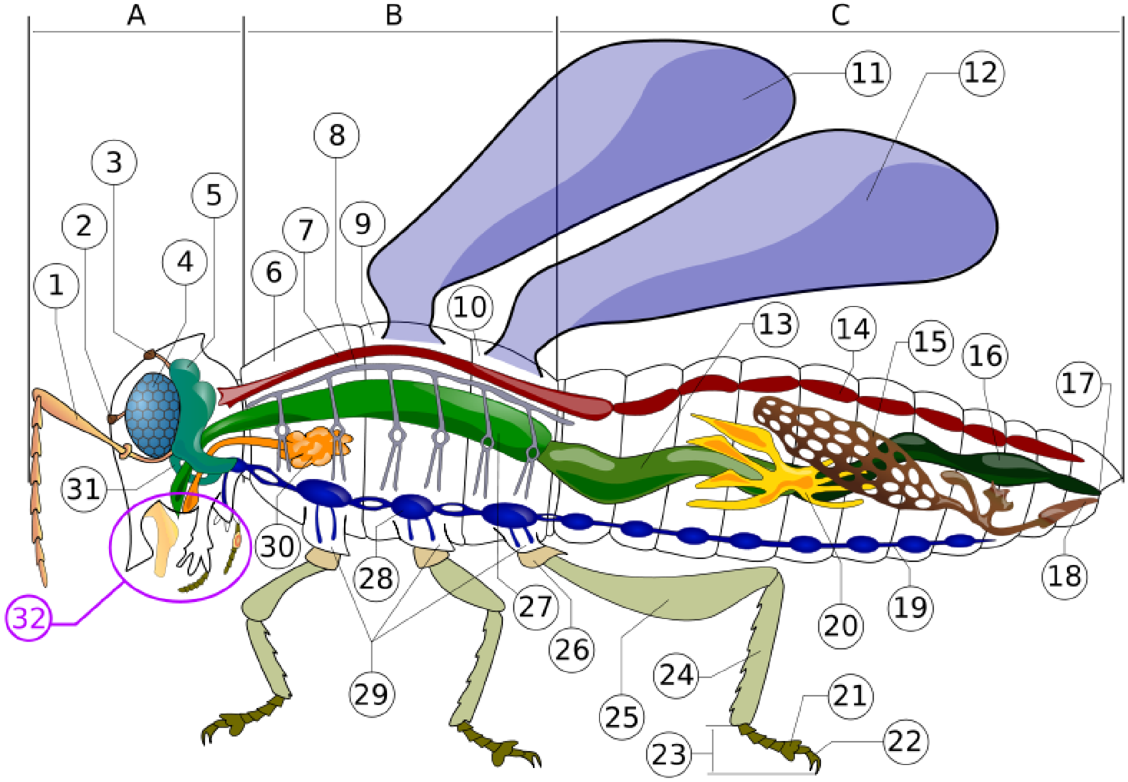
The life cycles of insects vary but most hatch from eggs. Insect growth is constrained by the inelastic exoskeleton and development involves a series of molts. The immature stages can differ from the adults in structure, habit and habitat and can include a passive pupal stage in those groups that undergo 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.

Morphology and physiology



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.

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.

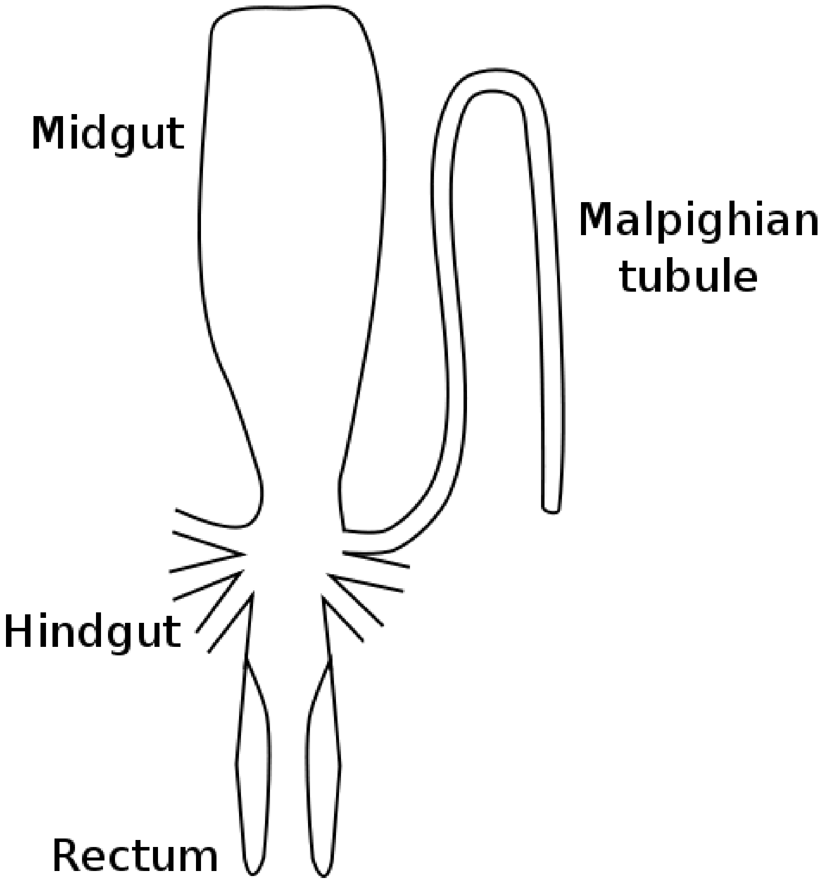
Digestive system

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.

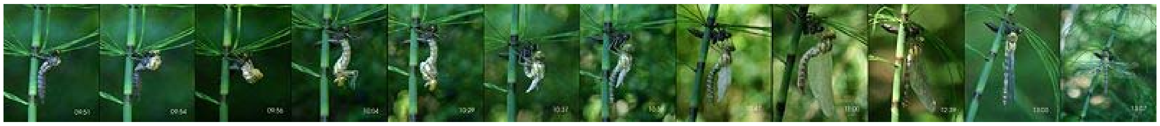
Metamorphosis

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

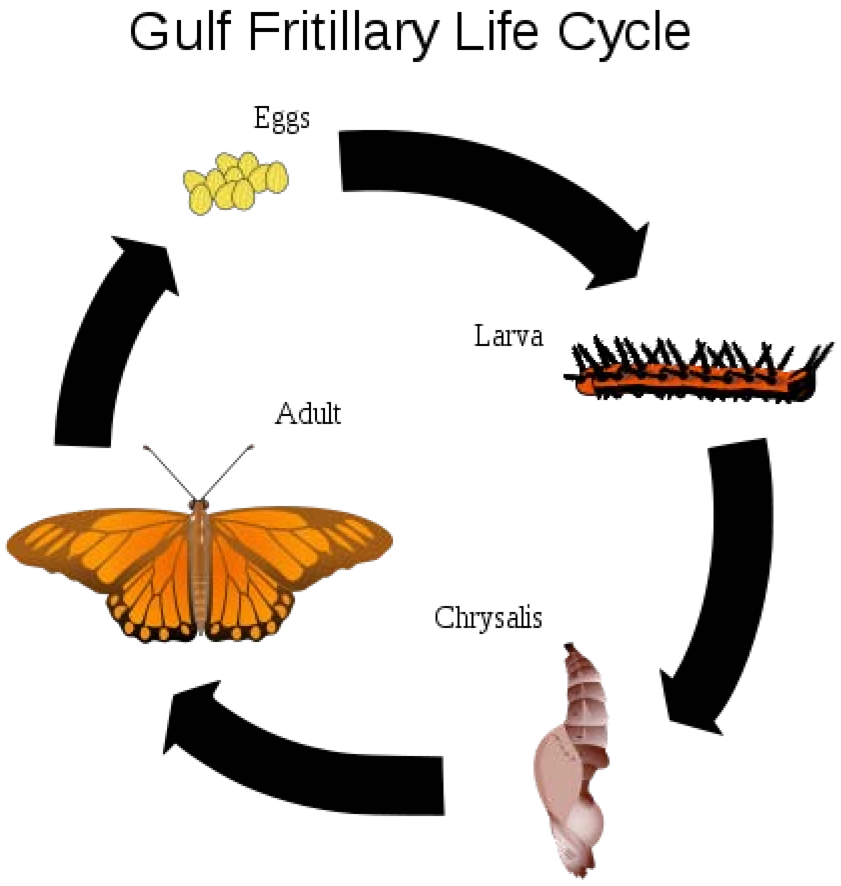
Insects that show hemimetabolism, or incomplete metamorphosis, change gradually by undergoing a series of molts. An insect molts when it outgrows its exoskeleton, which does not stretch and would otherwise restrict the insect's growth. The molting process begins as the insect's epidermis secretes a new 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.

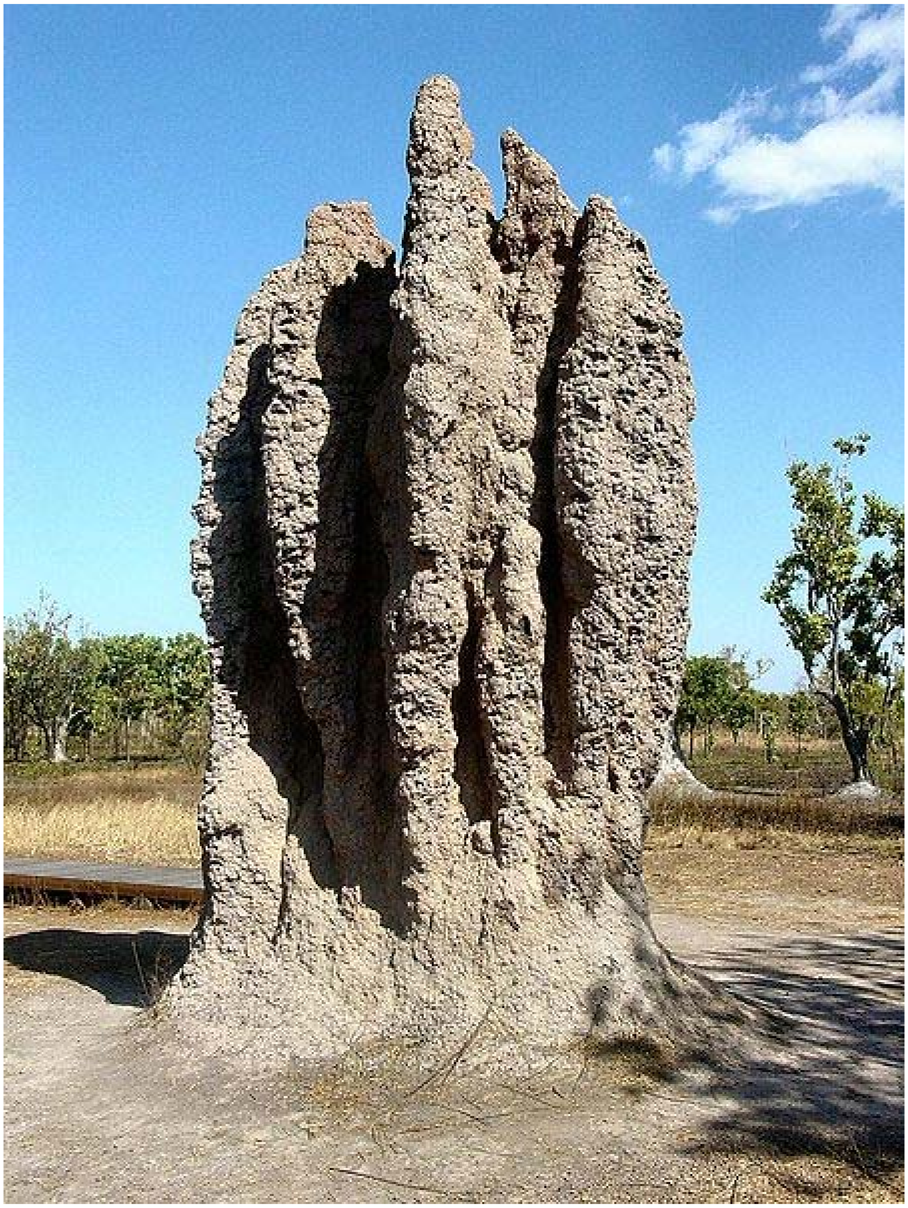
Communication using surface-borne vibrational signals is more widespread among insects because of size constraints in producing air-borne sounds. Insects cannot effectively produce low-frequency sounds, and high-frequency sounds tend to disperse more in a dense environment (such as foliage), so insects 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.

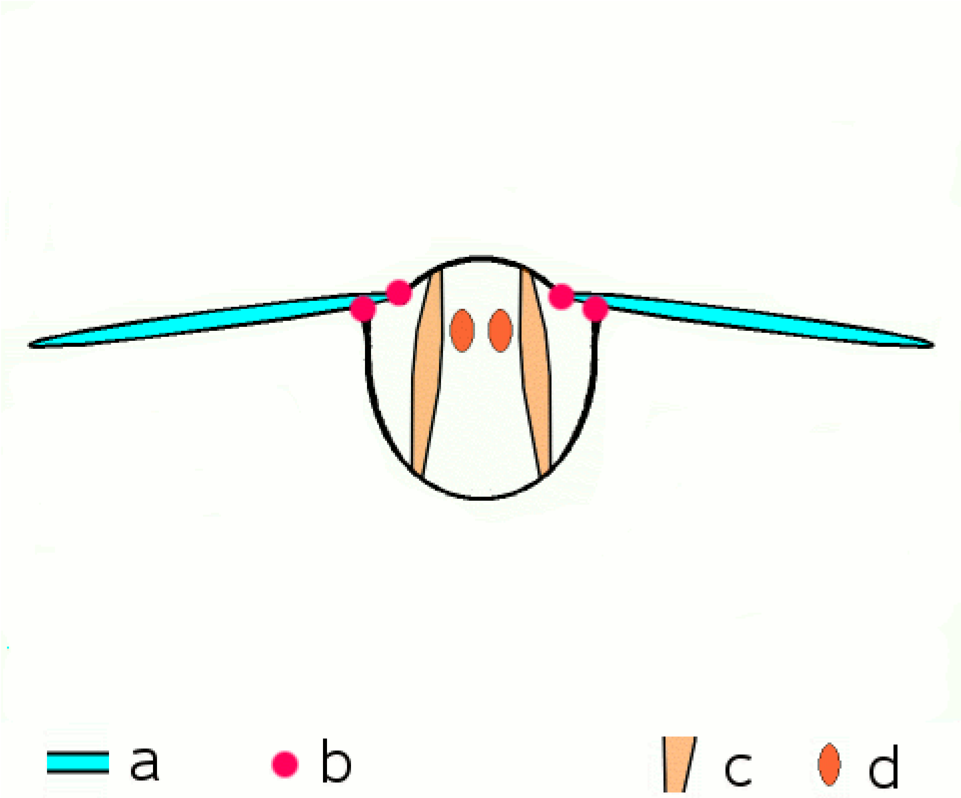
Only insects which live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to 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

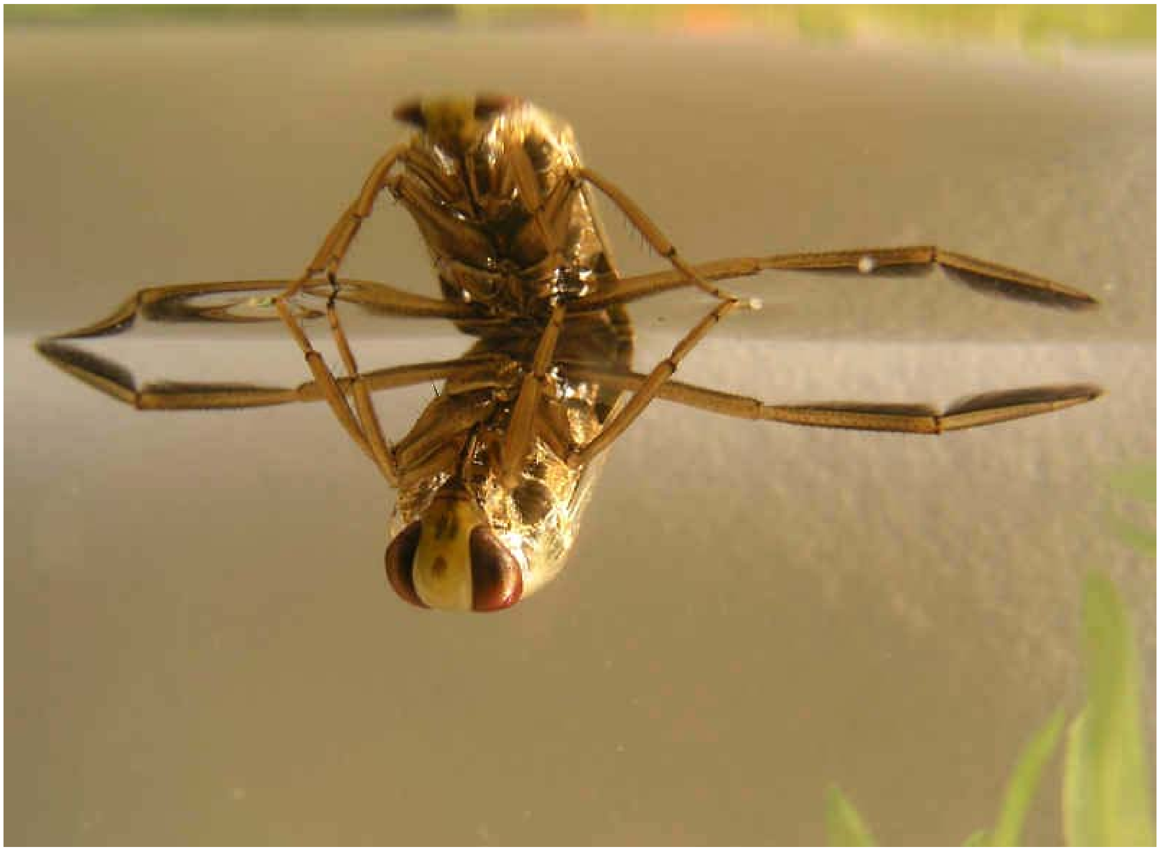
Many adult insects use six legs for walking and have adopted a tripedal gait. The tripedal gait allows for rapid walking while always having a stable stance and has been studied extensively in cockroaches. The legs are used in alternate triangles touching the ground. For the first step, the middle right 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*).

Evolution

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

Predation by vertebrates

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.

Coevolution with plants

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 and systematics

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 two primitively wingless orders: bristletails (Archaeognatha) and 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 separated 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.

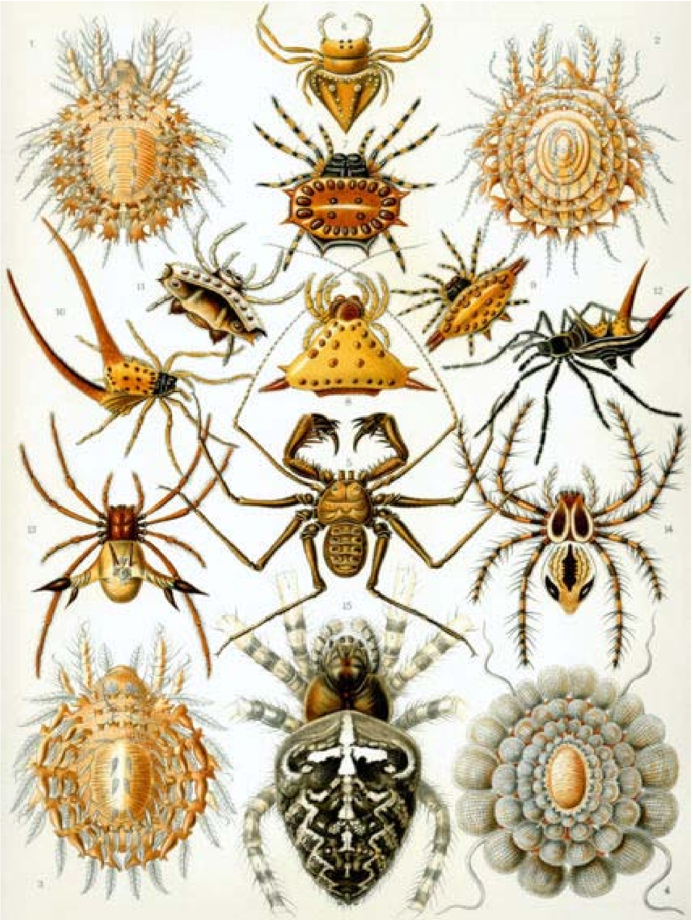
Entomophagy

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.

Chapter- 3

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

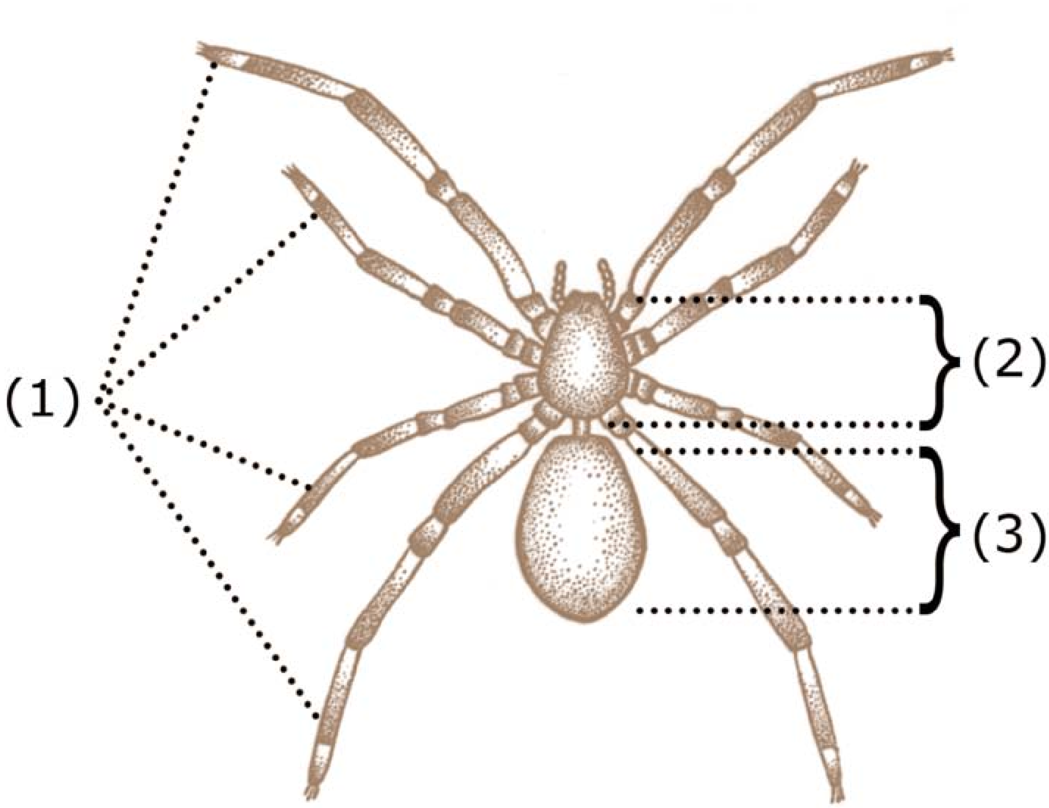
Extant orders

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 2005, over 6,300 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 hasn't 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- 4

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

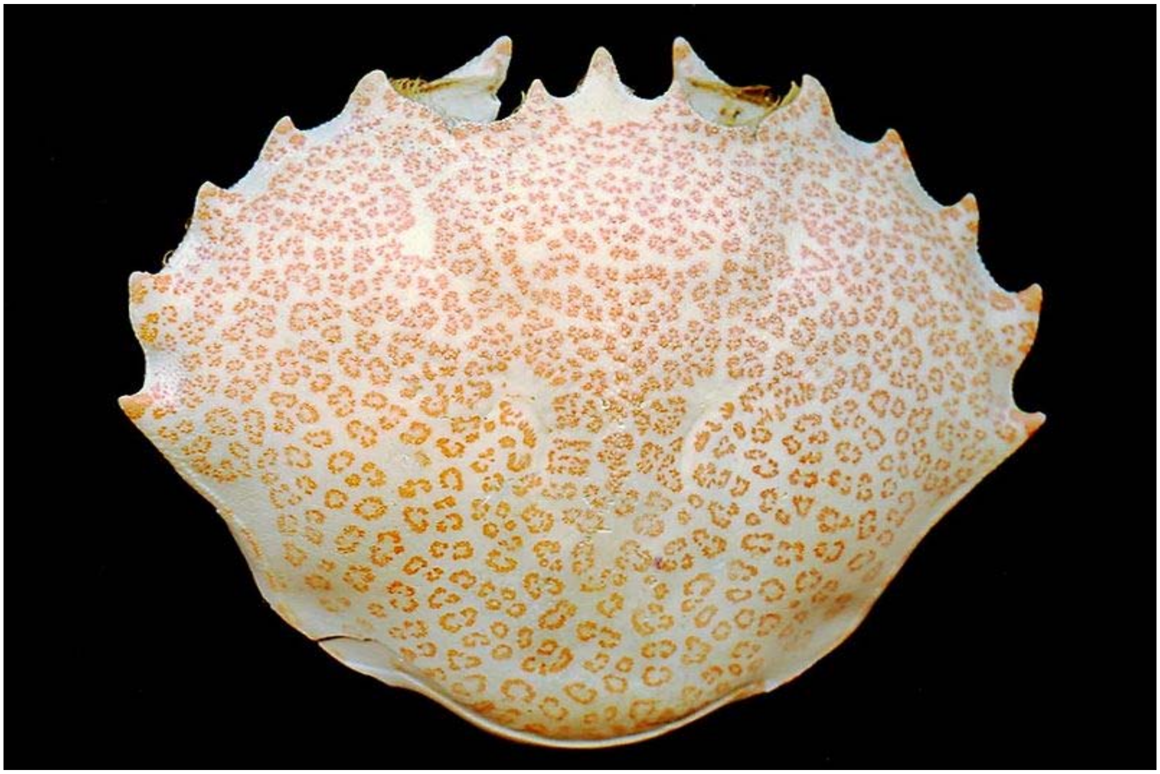
Malacostraca

  Phyllocarida
  Hoplocarida
  Eumalacostraca

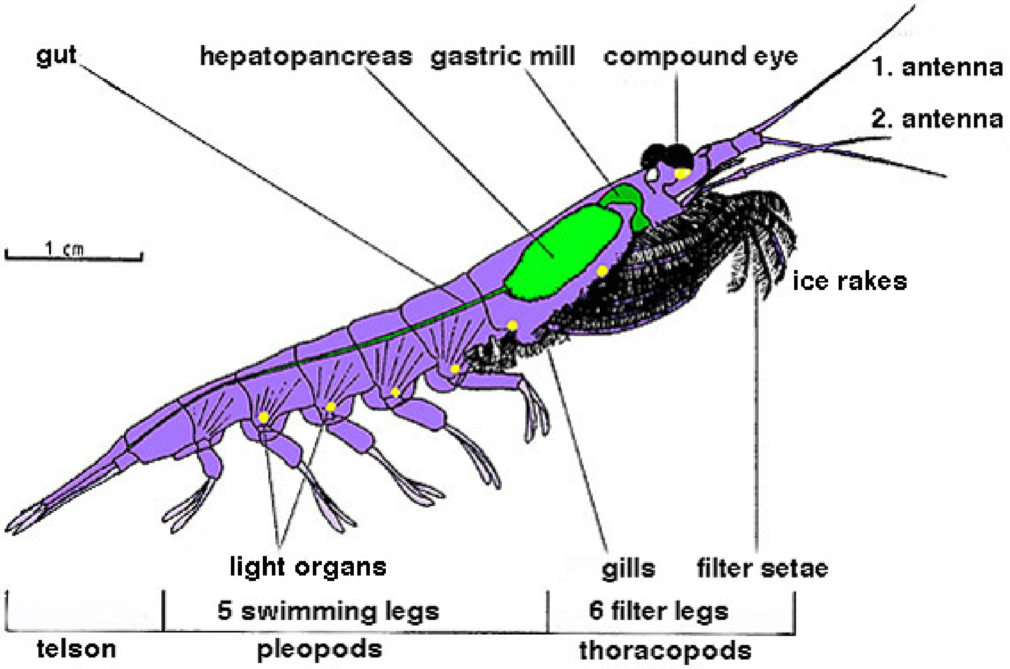
Crustaceans (**Crustacea**) form a very large group of arthropods, usually treated as a subphylum, which includes such familiar animals as crabs, lobsters, crayfish, shrimp, krill and barnacles. The 50,000 described species range in size from *Stygotantulus stocki* at 0.1 mm (0.004 in), to the Japanese 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

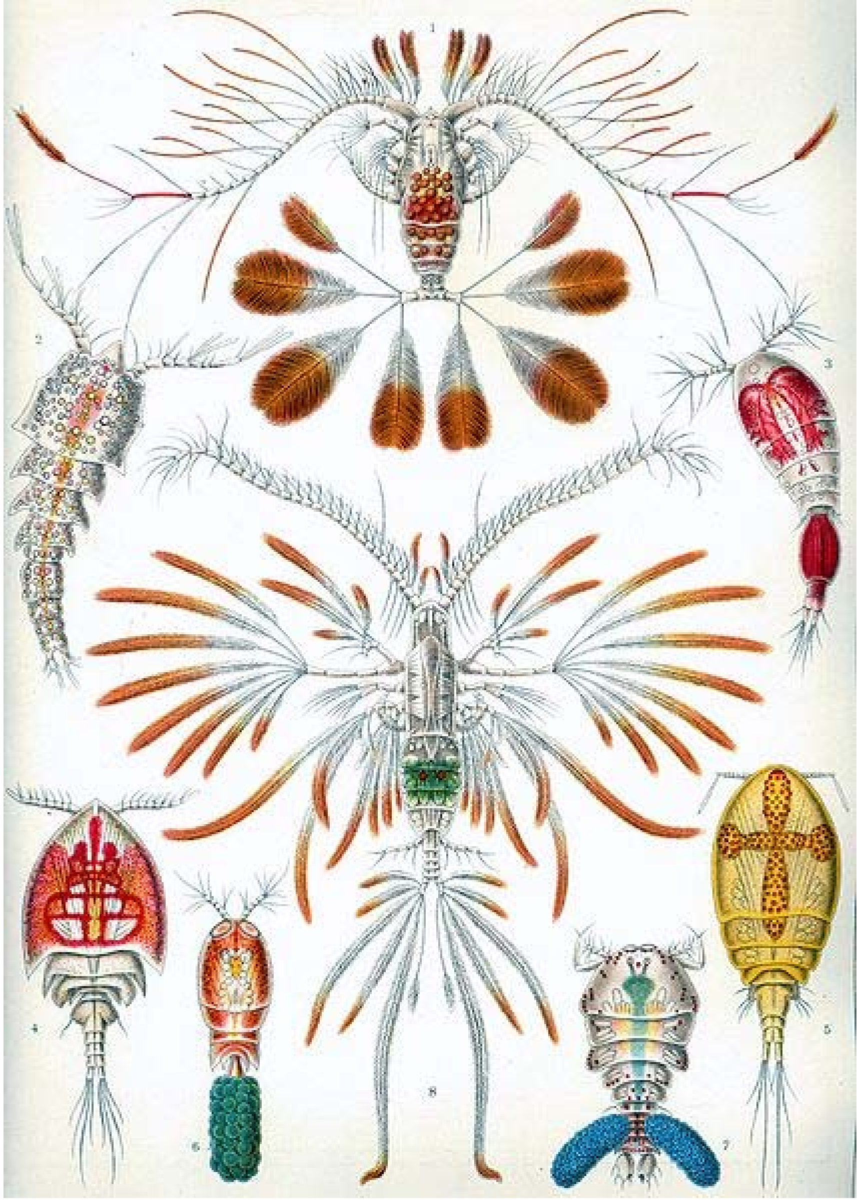
Crustaceans exhibit a number of larval forms, of which the earliest and most characteristic is the nauplius. This has three pairs of appendages, all emerging from the young animal's head, and a single naupliar eye. In most groups, there are further larval stages, including the zoea (pl. zoeæ or zoeas). 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

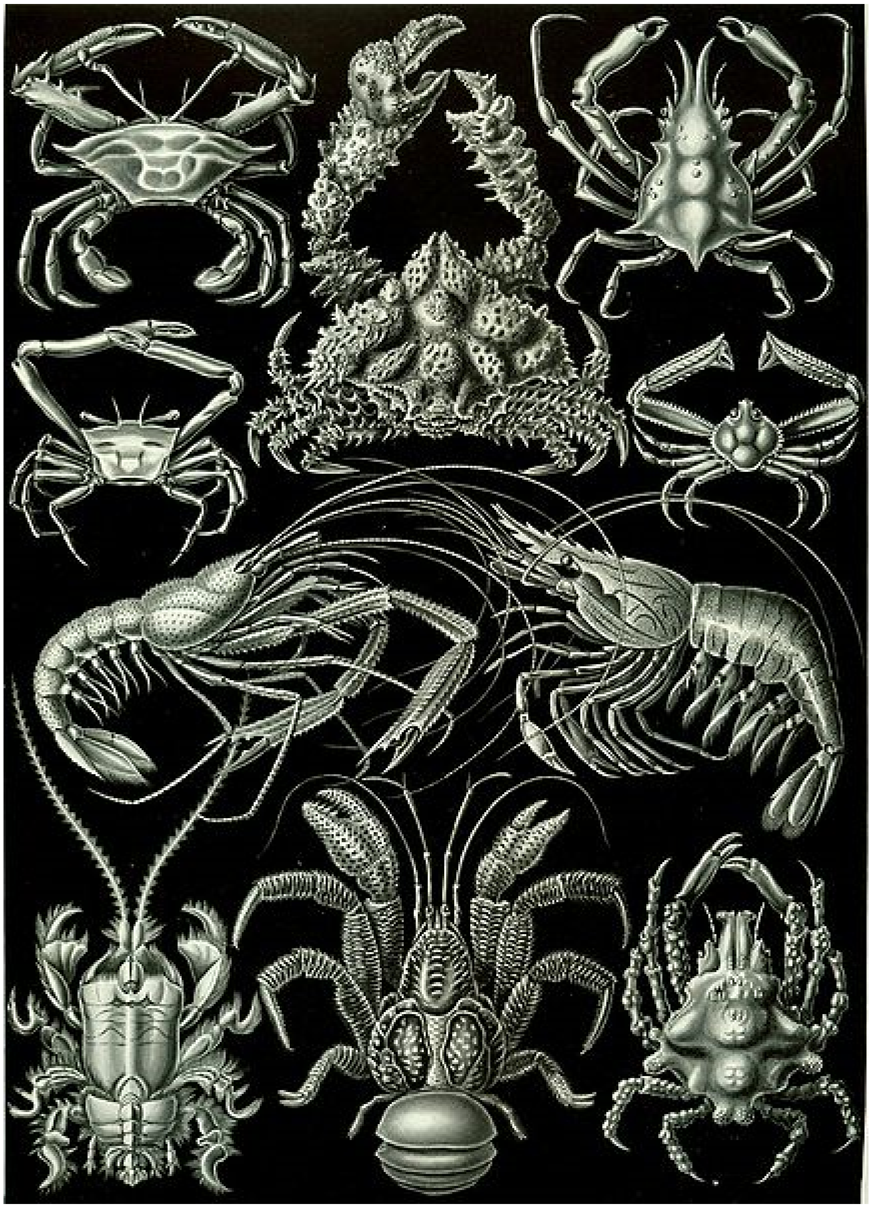
The name "crustacean" dates from the earliest works to describe the animals, including those of Pierre Belon and Guillaume Rondelet, but the name was not used by some later authors, including Carl Linnaeus, who included crustaceans among the "Aptera" in his *Systema Naturae*. The earliest nomenclaturally 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

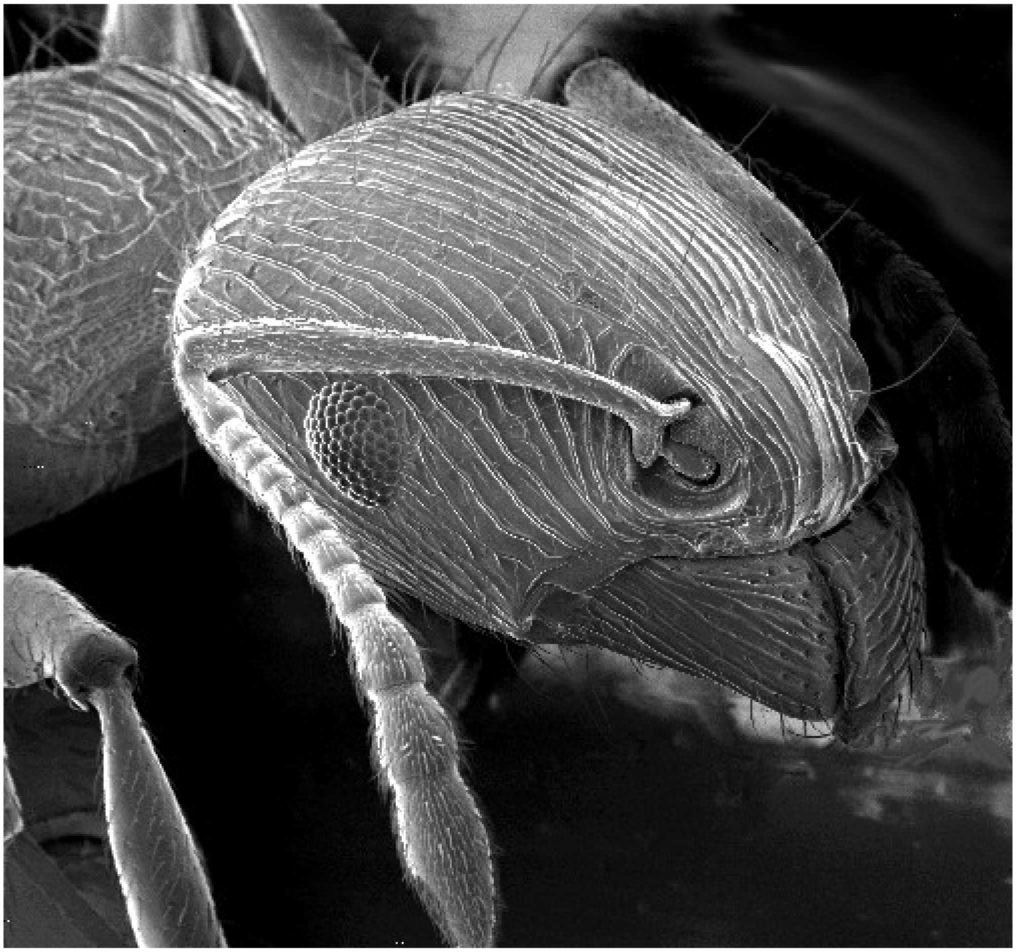
Crustaceans have a rich and extensive fossil record, which begins with animals such as *Canadaspis* and *Perspicaris* from the Middle Cambrian age Burgess Shale. Most of the major groups of crustaceans appear in the fossil record before the end of the Cambrian, namely the Branchiopoda, Maxillopoda (including 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.

Chapter- 5

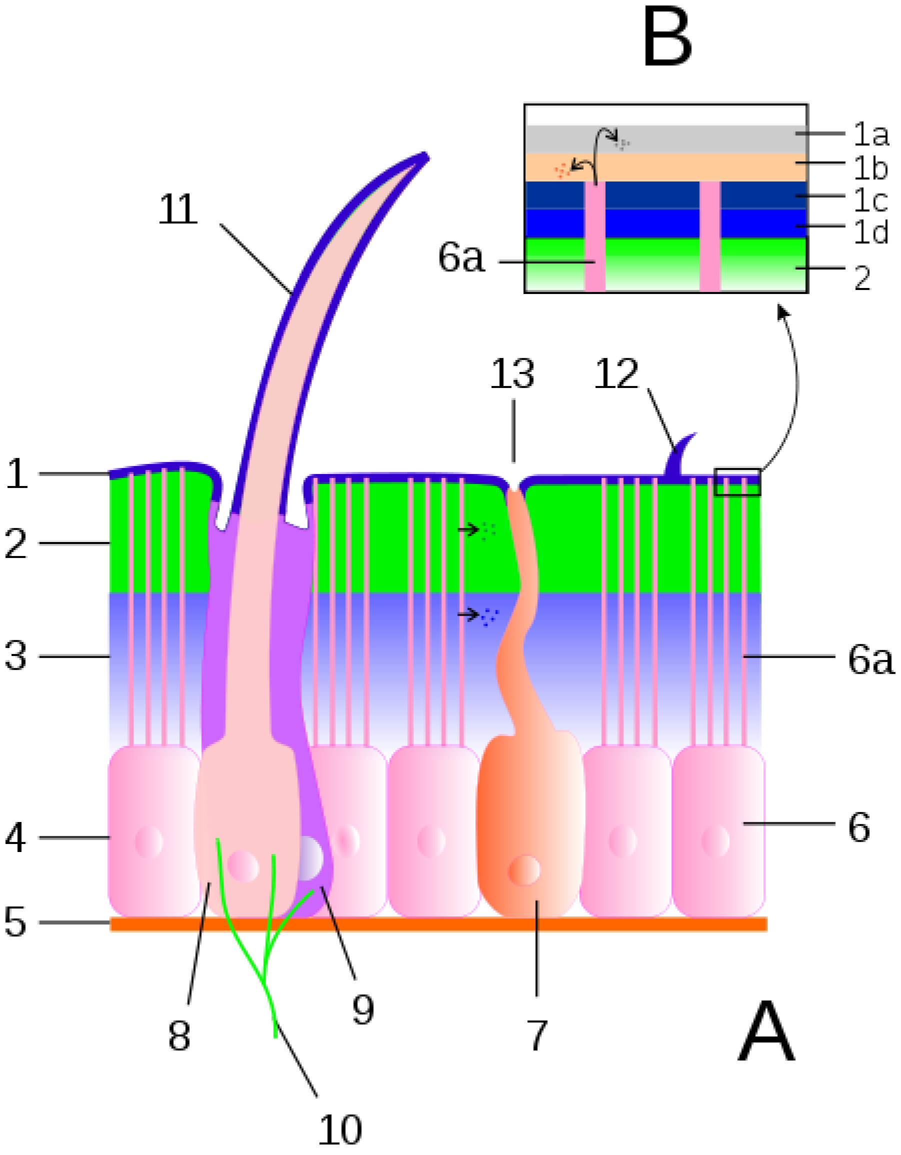
Arthropod Exoskeleton



The head of an ant: Chitin Type

Arthropods are covered with a tough or resistant **exoskeleton**, which may be mineralised or constructed of a tough polymer such as chitin. This external skeleton is moulted as the organism grows.

Microscopic structure



A: Cuticle and epidermis; **B**: Epicuticle detail . **1**: Epicuticle; **1a**: Cement layer; **1b**: Wax layer; **1c**: Outer epicuticle; **1d**: Inner epicuticle. **2**: Exocuticle; **3**: Endocuticle; **2+3**: Procuticle; **4**: Epidermis; **5**: Basement membrane; **6**: epidermic cell; **6a**: Pore canal; **7**: Glandular cell; **8**: Trichogen cell; **9**: Tormogen cell; **10**: Nerve; **11**: Sensilia; **12**: Hair; **13**: Gland opening.

A typical arthropod exoskeleton is a multi-layered structure with four functional regions: epicuticle, procuticle, epidermis and basement membrane. Of these, the epicuticle is a multi-layered external barrier that, especially in terrestrial arthropods, acts as a barrier against desiccation. The strength of the exoskeleton is provided by the underlying procuticle, which is in turn secreted by the epidermis. Arthropod cuticle is a biological composite material, consisting of two main portions: fibrous chains of alpha-chitin within a matrix of silk-like and globular proteins, of which the most well-known is the rubbery protein called resilin. The relative abundance of these two main components varies from approximately 50/50 to 80/20 chitin protein, with softer parts of the exoskeleton having a higher proportion of chitin. Although the cuticle is relatively soft when first secreted, it soon hardens in a poorly-understood process that involves dehydration and/or tanning mediated by hydrophobic chemicals called phenolics. Different types of interaction between the proteins and chitin leads to varying mechanical properties of the exoskeleton.

In addition to the chitino-proteinaceous composite of the cuticle, many crustaceans, some myriapods and the extinct trilobites further impregnate the cuticle with mineral salts, above all calcium carbonate, which can make up up to 40% of the cuticle. This can lead to great mechanical strength.

Mechanical properties

The two layers of the cuticle have different properties. The outer, sclerosed layer is very strong under compressive forces, but much weaker under tension. When it fails, it does so by cracking. The inner layer is not sclerosed, and is thus much softer; it is able to resist tensile forces but is liable to failure under compression.

This combination is especially effective in resisting predation, as predators tend to exert compression on the outer layer, and tension on the inner.

The degree of scleritisation affects how the cuticle responds to deformation. Below a certain point - and this point will be higher the more scleritised the cuticle is - deformation is elastic and the original shape is returned to after the stress is removed. Above this point, plastic (non-reversible) deformation occurs until finally the cuticle cracks.

Segmentation

The arthropod exoskeleton is typically divided into different functional units to allow flexibility in an often otherwise rigid structure. For example, the head is a fused capsule; and the trunk is often divided into a series of articulating sclerites called tergites. In addition, the characteristic limbs of arthropods need to be jointed. The internal surface of the exoskeleton is often elaborated into a set of specialised structures called apodemes that allow the attachment of muscles. Such endoskeletal components of the arthropod skeleton can be highly complex, as in crabs and lobsters.

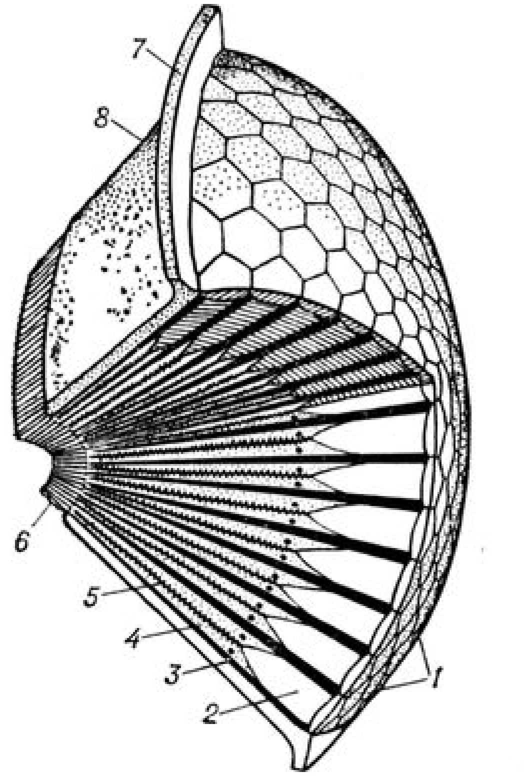
Ecdysis

Time series photos of a *Tibicen* Dog Day Cicada moulting in Ohio USA.

The relative rigidity of the exoskeleton means that continuous growth of arthropods is not possible. Therefore, growth is periodic and concentrated into a period of time when the exoskeleton is shed, called moulting or ecdysis, which is under the control of a hormone called ecdysone. Moulting is a complex process that is invariably dangerous for the arthropod involved. Before the old exoskeleton is shed, the cuticle separates from the epidermis through a process called apolysis. New cuticle is excreted by the underlying epidermis, and mineral salts are usually withdrawn from the old cuticle for re-use. After the old cuticle is shed, the arthropod typically pumps up its body (for example, by air or water intake) to allow the new cuticle to expand to a larger size: the process of hardening by dehydration of the cuticle then takes place. Newly molted arthropods typically appear pale or white, and darken as the cuticle hardens.

Chapter- 6

Arthropod Eye



Anatomy of the compound eye of an insect

The arthropods ancestrally possessed compound eyes, but the type and origin of this eye varies between groups, and some taxa have secondarily developed simple eyes. The organ's development through the lineage can be estimated by comparing groups that branched early, such as the velvet worm and horseshoe crab to the advanced eye condition found in insects and other derived arthropods.

Apposition eyes are the most common form of eye, and are presumably the ancestral form of compound eye. They are found in all arthropod groups, although they may have evolved more than once within this phylum. Some annelids and bivalves also have apposition eyes. They are also possessed by *Limulus*, the horseshoe crab, and there are suggestions that other chelicerates developed their simple eyes by reduction from a compound starting point. (Some caterpillars appear to have evolved compound eyes from simple eyes in the opposite fashion.)

Eyes and functions

Most arthropods have at least one of two types of eye: lateral compound eyes, and smaller median ocelli. The two eye types are used in concert, because each has its own advantage. Insects can function well with either type of eye surgically removed, but the two types combine to give better performance. Ocelli can detect lower light levels, and have a faster response time, while compound eyes are better at detecting edges and objects.

Genetic controls

The head patterning is controlled by *orthodenticle*, a homeobox gene which demarkates the segments from the top-middle of the head to the more lateral aspects. The ocelli are in an orthrodenticle-rich area, and the gene is not expressed by the time one gets as lateral as the compound eyes.

The gene *dachshund* is involved in the development of the compound eye.

Different opsins are used in the ocelli to the compound eyes.

Evolution

Hexapods are currently thought to fall within the Crustacean crown group; while molecular work paved the way for this association, their eye morphology and development is also markedly similar. The eyes are strikingly different from the myriapods, which were traditionally considered to be a sister group to the hexapoda.

Both ocelli and compound eyes were probably present in the last common arthropod ancestor, and may be apomorphic with ocelli in other phyla, such as the annelids. Median ocelli are present in chelicerates and mandibulates; lateral ocelli are also present in chelicerates.

Origin

No fossil organisms have been identified as similar to the last common ancestor of arthropods; hence the eyes possessed by the first arthropod remains a matter of conjecture. The largest clue into their appearance comes from the onychophorans: a stem group lineage that diverged soon before the first true arthropods. The eyes of these creatures are attached to the brain using nerves which enter into the centre of the brain, and there is only one area of the brain devoted to vision. This is similar to the wiring of the median ocelli (small simple eyes) possessed by many arthropods; the eyes also follow a similar pathway through the early development of organisms. This suggests that onychophoran eyes are derived from simple ocelli, and the absence of other eye structures implies that the ancestral arthropod lacked compound eyes, and only used median ocelli to sense light and dark. However, a conflicting view notes that compound eyes appeared in many early arthropods, including the trilobites and eurypterids, suggesting that the compound eye may have developed after the onychopohran and arthropod lineages split, but before the radiation of arthropods. This view is supported if a stem-arthropod position is supported for compound-eye bearing Cambrian organisms such as the Anomalocaridids. An alternative, however, is that compound eyes evolved multiple times among the arthropods.

There were probably only a single pair of ocelli in the arthropod concestor; Cambrian lobopod fossils display a single pair, and while many arthropods today have three, four, or even six, the lack of common pathway suggests that a pair is the most probable ancestral state. The crustaceans and insects mainly have three ocelli, suggesting that such a formation was present in *their* concestor.

It is deemed probable that the compound eye arose as a result of the 'duplication' of individual ocelli. In turn, the disperseal of compound eyes seems to have created large networks of seemingly independent eyes in some arthropods, such as the larvae of certain insects. In some other insects and myriapods, lateral ocelli appear to have arisen by the reduction of lateral compound eyes.

Trilobite eyes

The eyes of trilobites were of two forms, both of which grew by the addition of new ommatidia at the bottom of the eye, a row at a time. This growth form is today unique to the horseshoe crabs. The holochroal eye, consisting of many small lenses, appears to be the ancestral state. The more complex schizochroal eye was more derived.

Limulus

Limulus, the horseshoe crab, has traditionally been used in investigations into the eye, because it has relatively large ommatidia with large nerve fibres (making them easy to experiment on). It also falls in the stem group of the chelicerates; its eyes are believed to represent the ancestral condition because they have changed so little over evolutionary time. Indeed the horseshoe crabs are often considered to be living fossils. Most other living chelicerates have lost their lateral compound eyes, evolving simple eyes in their place.

Limulus has two large compound eyes on the sides of its head. An additional simple eye is positioned at the rear of each of these structures. In addition to these obvious structures, it also has two smaller ocelli situated in the middle-front of its carapace, which may superficially be mistaken for nostrils. A further simple eye is located beneath these, on the underside of the carapace. A further pair of simple eyes are positioned just in front of the mouth. The simple eyes are probably important during the embryonic or larval stages of the organism, with the compound eyes and median ocelli becoming the dominant sight organisms during adulthood. These ocelli are less complex, and probably less derived, than those of the mandibulata. Unlike the trilobites', the compound eyes of *Limulus* are triangular in shape; they also have a generative region at their base, but this elongates with time. Hence the one ommatidium at the apex of the triangle was the original "eye" of the larval organism, with subsequent rows added as the organism grew.

Insects & Crustaceans

These two groups are probably monophyletic; their eyes certainly develop in a very similar fashion. Their larvae only possess a pit-eye ocellus, termed Bolwig's organ. The compound eyes of adults develop in a separate region of the head. New ommatidia are added in semicircular rows at the rear of the eye; during the first phase of growth, this leads to individual ommatidia being square, but later in development they become hexagonal. The hexagonal pattern will only become visible when the carapace of the stage with square eyes is molted.

Myriapods

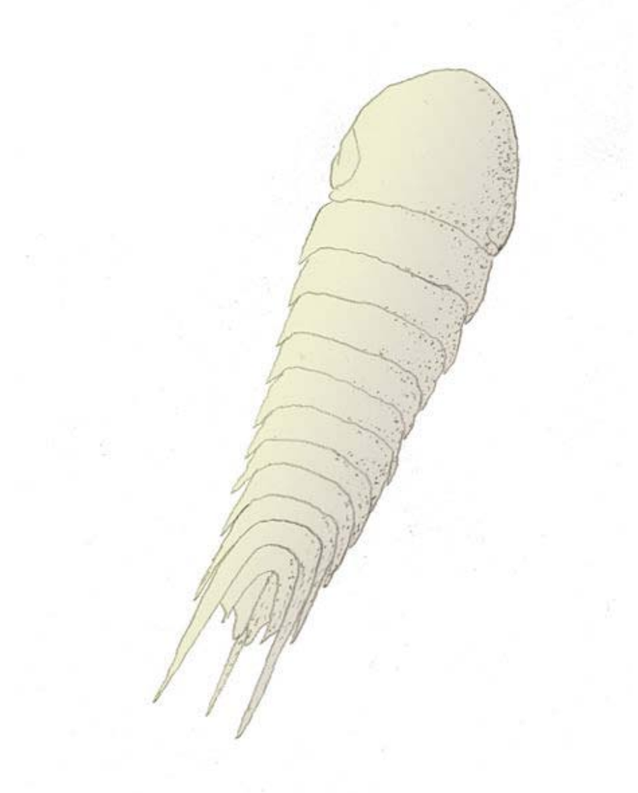
Most myriapods bear stemmata - that is, single lensed eyes which evolved by the reduction of a compound eye. However, the genus *Scutigera* has secondarily re-evolved a compound eye composed of repeated stemmata. These appear to grow in rows which are inserted between existing rows of ocelli.

Chapter- 7

Prehistoric Arthropods

Acanthomeridion

Acanthomeridion serratum



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
(unranked):	*incertae sedis*
Family:	**Acanthomeridiidae**

	Hou & Bergström, 1997
Genus:	***Acanthomeridion*** Hou, Chen & Lu, 1989
Species:	***A. serratum***

Binomial name

Acanthomeridion serratum
Hou, Chen & Lu, 1989

Acanthomeridion is an extinct arthropod found in the Chengjiang fauna deposits of China. In 1997, it was placed in its own, monotypic family, **Acanthomeridiidae**.

Arthropleuridea

Arthropleuridea
Fossil range: Silurian–Permian

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Myriapoda
Class:	Diplopoda?
Subclass:	**†Arthropleuridea**

Orders

Arthropleurida
Eoarthropleurida
Microdecemplicida

Arthropleuridea was a class of arthropods that flourished during the Carboniferous period. Members are defined by diplosomy, paranotal tergal lobes separated from the axis by a suture, and by sclerotized plates buttressing the leg insertions. Despite their unique features, recent phylogenetic research suggests that Arthropleuridea may be included among millipedes. The class contains three recognized orders, each with a single genus. Arthropleurids had about 30 pairs of legs, whose tracks have been found in the Joggins deposit in Nova Scotia, Canada.

Arthropleuridea is most famous for order Arthropleurida. With the genus *Arthropleura* over 2 meters in length, arthropleurids are among the largest arthropods ever to have lived. The lack of large terrestrial vertebrate predators and the highly oxygenic atmosphere at that time probably enabled them to grow so large. Arthropleurids lived in the moist coal swamps that were common at the time and may have burrowed in the undergrowth. They were either herbivores or detritivores. Besides their size, their most distinguishing features were their legs with eight segments (as many as 30 pairs) and extremely tough exoskeletons. There is no evidence of spiracles, so the animals must have used lungs or gills for respiration. Arthropleurids became extinct as the climate became drier and the coal swamps dried out.

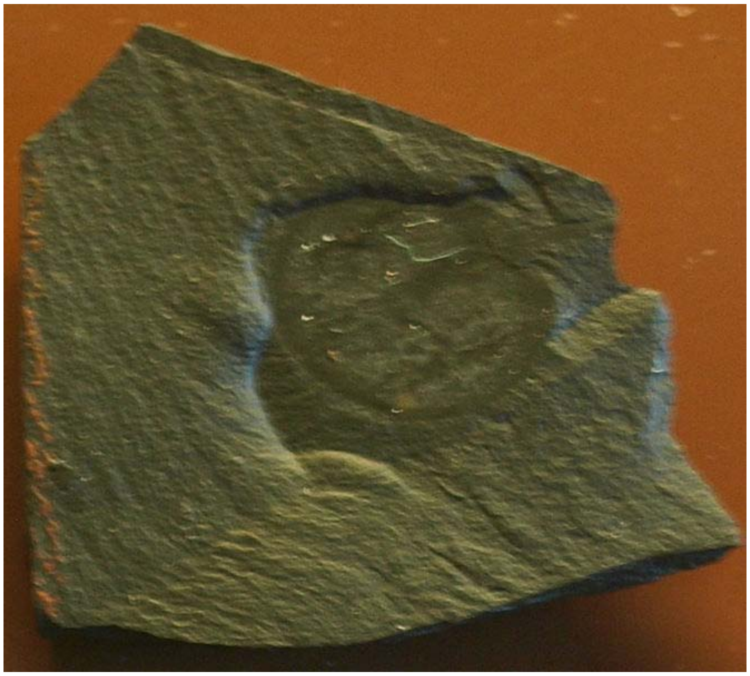
Tracks from *Arthropleura* up to 50 cm wide have been found at Joggins, Nova Scotia.

Most arthropleurids are thought to have been terrestrial, although, without any known respiratory structure, terrestriality is assumed only by analogy to modern arthropods. Early forms, however, including order Eoarthropleurida, appear to have been aquatic. For this reason, some question Arthropleuridea's inclusion among millipedes because no modern aquatic myriapods are known. Eoarthropleurida has been found from the Upper Silurian through the Upper Devonian of Europe and North America.

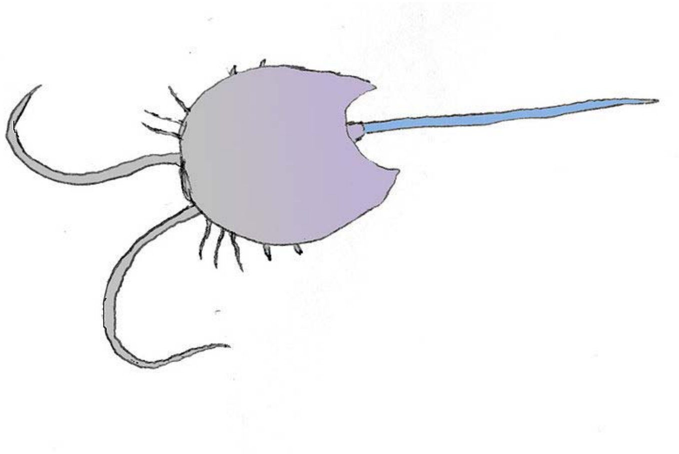
Order Microdecemplicida was smaller in comparison to the other arthropleurids, with genus *Microdecemplex* just a few millimeters long. It is known from the Middle through Upper Devonian of New York state.

Burgessia

Burgessia
Fossil range: Mid Cambrian



B. bella



Reconstruction of *Burgessia*

Scientific classification	
Kingdom:	Animalia
Genus:	***Burgessia***

Burgessia is an extinct genus of arthropod from the Middle Cambrian. Its fossils have been found in the Burgess Shale in British Columbia, Canada. 1383 specimens of *Burgessia* are known from the Greater Phyllopod bed, where they comprise 2.63% of the community.

Dolichopterus

Dolichopterus **Fossil range: Late Silurian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	†Eurypterida
Family:	†Dolichopteridae
Genus:	†***Dolichopterus*** Hall, 1859
Diversity	
4–5 species	

Dolichopterus is a genus of the prehistoric sea scorpions, arthropods in the class Eurypterida.

Distribution

It lived in the Late Silurian (around 420 million years ago) in shelf or epicontinental seas of the region where Avalonia, Baltica and Laurentia met during the Caledonian orogeny; its fossils have been found in modern-day North America and the Baltic region. They were about 25–30 centimetres (10–12 in) long.

Relatives

Strobilopterus probably was one of the closest relatives of *Dolichopterus*, but overall the phylogeny and systematics of the family Dolichopteridae is disputed: some place it closer to the Eurypteridae, while others assign it to the second lineage of sea scorpions which contains the Stylonuridae.

Description

Dolichopteridae, which lived in the Silurian and Devonian periods, had outer surfaces that were either smooth with pustules and semilunar scales. Their compound eyes were arcuate and located anteriorly on the prosoma (head). Their abdomens had epimers (lateral projections). The telson, (tail) was lanceolate. Their chelicerae were small, and the first three pairs of walking lags were stout, with powerful spines. The last pair of walking lags had supplementary lobes, while the swimming lags had the last joint enlarged, as part of the paddle. The male genital appendage was long.

Dolichopterus is distinguishable by its nearly smooth outer surface; its subquadrate prosoma (head), and the slightly serrated margins on the distal joints and lobes of the swimming legs.

Species

The following species have been named:

- *Dolichopterus gotlandicus* Kjellesvig-Waering, 1979 – Sweden
- *Dolichopterus jewetti* Caster & Kjellesvig-Waering, 1956 – USA
- *Dolichopterus macrocheirus* Hall, 1859 (type species) – USA, Canada
- *Dolichopterus siluriceps* Clarke & Ruedemann, 1912 – USA, Canada
- ?*Dolichopterus stoermeri* Caster & Kjellesvig-Waering, 1956 – Estonia

Trilobite

Trilobites
Temporal range: Atdabanian – Late Permian

Kainops invius

Scientific classification

Kingdom:	Animalia
Phylum:	**Arthropoda** 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.

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

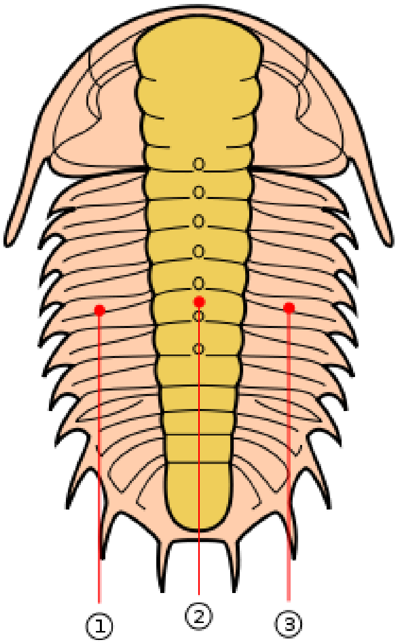
Cast of *Isotelus rex*, the largest known trilobite.

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.

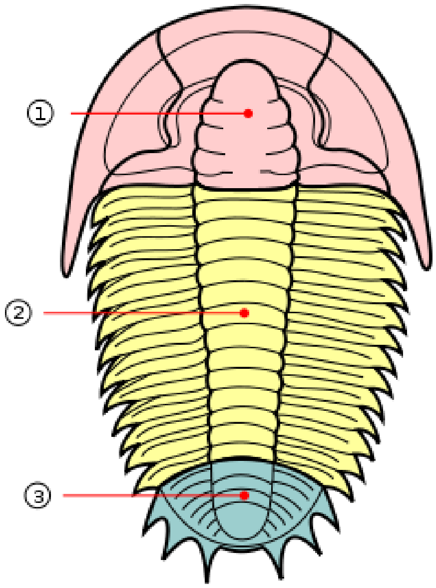
Trilobites range in length from 1 millimetre (0.04 in) to 72 centimetres (28 in), with a typical size range of 3–10 cm (1.2–3.9 in). The world's largest trilobite, *Isotelus rex*, was found in 1998 by Canadian scientists in Ordovician rocks on the shores of Hudson Bay.

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.

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)

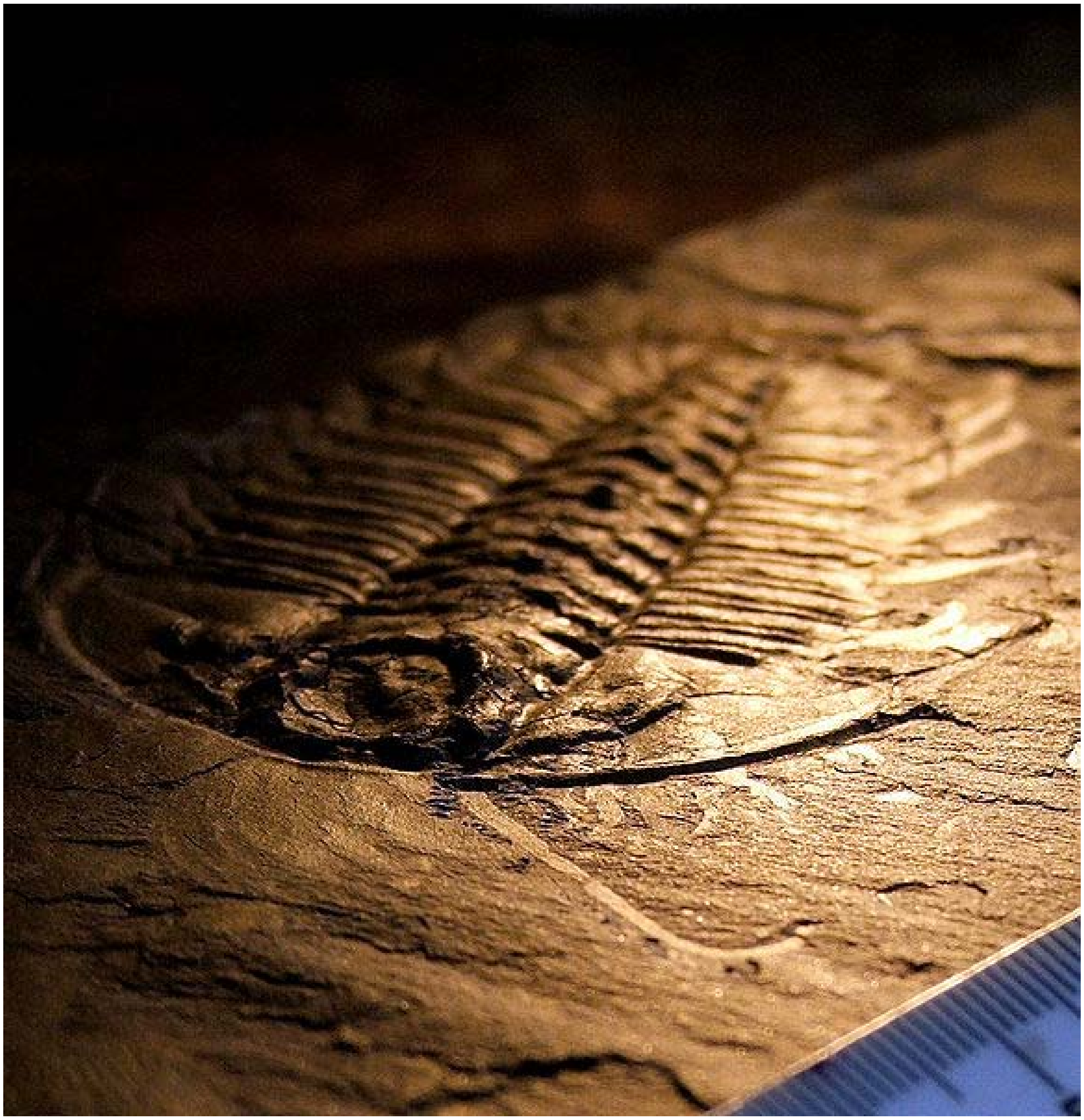
Trilobite exoskeletons show a variety of small-scale structures collectively called prosopon. Prosopon does not include large scale extensions of the cuticle (e.g. hollow pleural spines) but to finer scale features, such as ribbing, domes, pustules, pitting, ridging and perforations. The exact purpose 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 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.

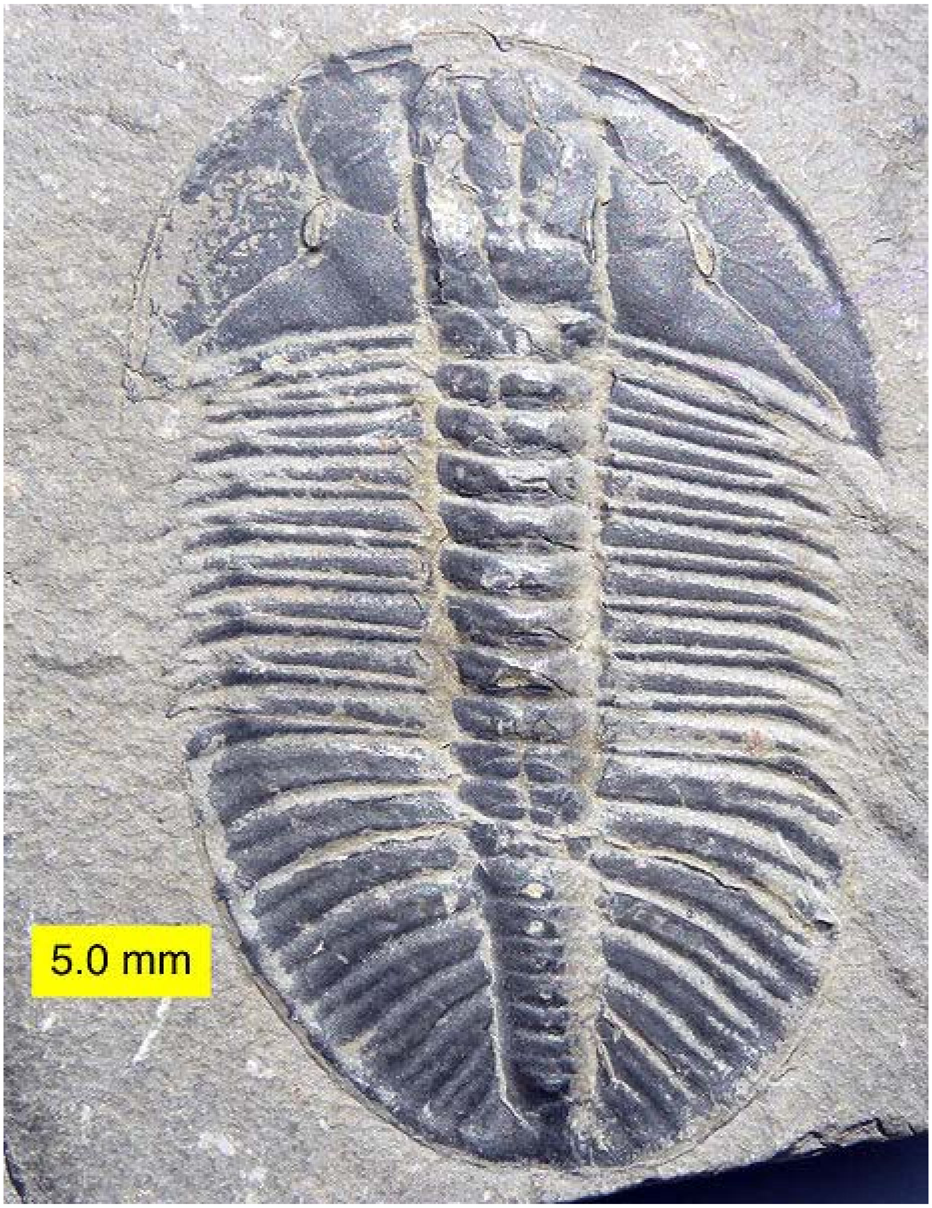
Evolutionary trends

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

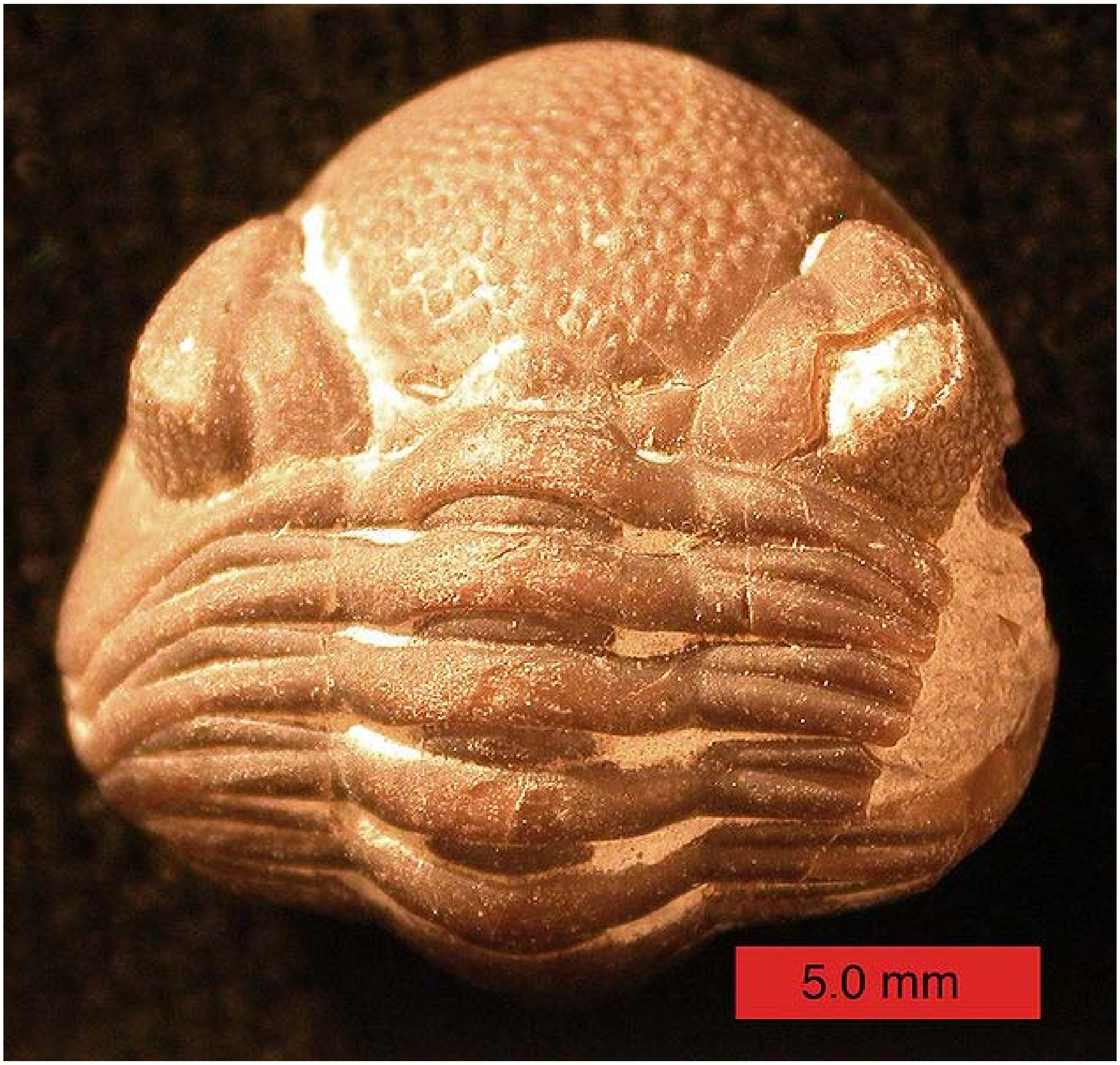
Very shortly after trilobite fossils appeared in the lower Cambrian, they rapidly diversified into the major orders that typified the Cambrian - Redlichiida, Ptychopariida, Agnostida and Corynexochida. The first major crisis in the trilobite fossil record occurred in the Middle Cambrian, surviving orders 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.

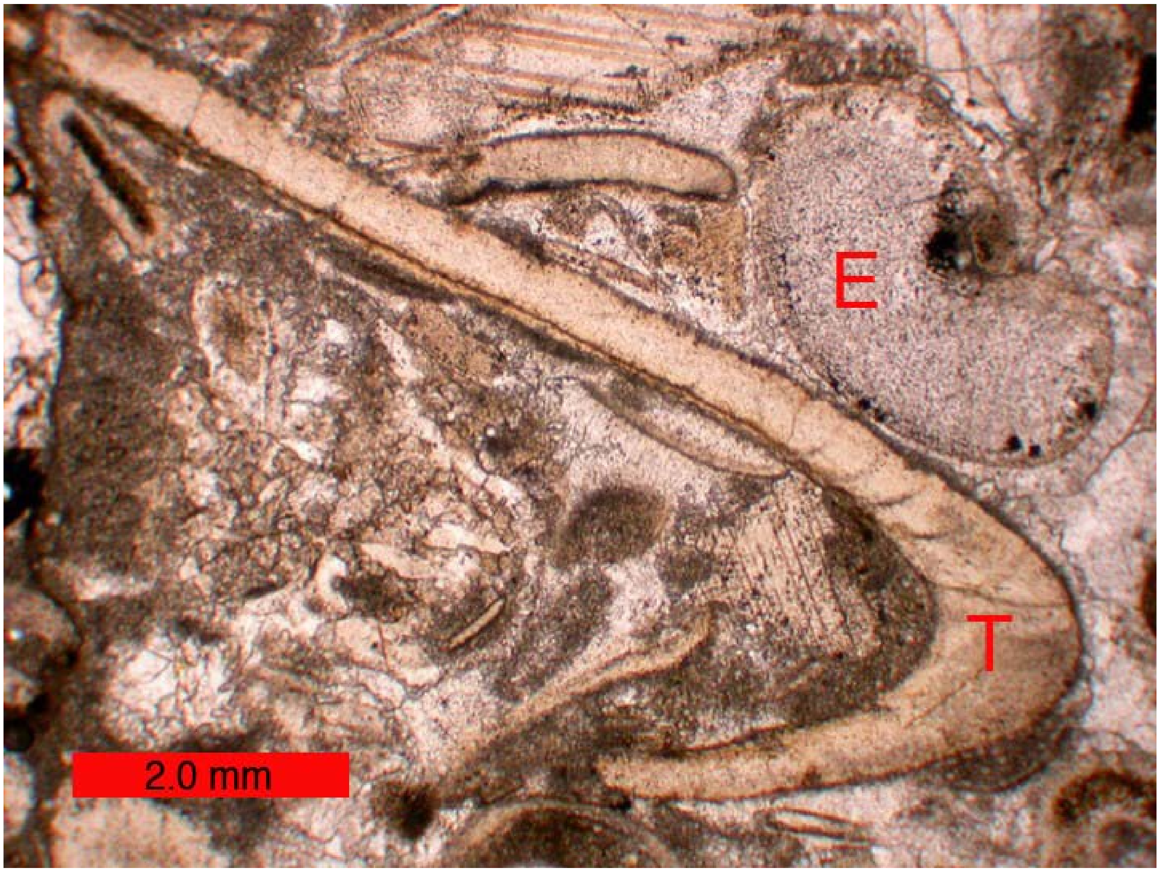
Final extinction

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.