



Chelicerata
(Animal Subphylum)

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Chapter 1

Chelicerata

Chelicerata
Temporal range: 445–0 Ma
Late Ordovician – Recent



Horseshoe crab underside

Scientific classification

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: **Chelicerata**
Heymons, 1901

Classes

- Arachnida
- Pycnogonida
- Merostomata

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

Like all arthropods, chelicerates have segmented bodies with jointed limbs, all covered in a cuticle made of chitin and proteins. The chelicerate bauplan consists of two tagmata, the

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

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

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

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

Description

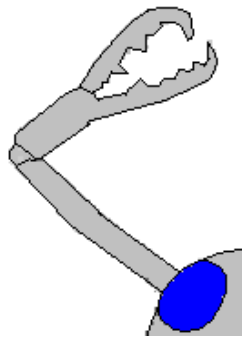
Segmentation and cuticle

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

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

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

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



The chelicera of a eurypterid.



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

Chelicerae and pedipalps

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

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

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

Body cavities and circulatory systems

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

Respiratory systems

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

vertically-oriented book gills whose internal structure is very similar to that of scorpions' book lungs.

Feeding and digestion

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

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

Excretion

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

Nervous system

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

	only	
Other arachnids	All	All

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

Senses

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

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

Reproduction



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

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

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

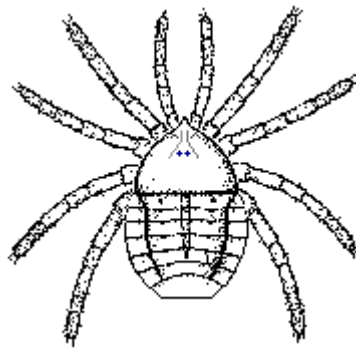
Levels of parental care for the young range from zero to prolonged. Scorpions carry their young on their backs until the first molt, and in a few semi-social species the young remain with their mother. Some spiders care for their young, for example a wolf spider's brood cling to rough bristles on the mother's back, and females of some species respond

to the "begging" behavior of their young by giving them their prey, provided it is no longer struggling, or even regurgitate food.

Evolutionary history

Fossil record

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



Palaeotarbus jerami, a trigonotarbid and the oldest known arachnid

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

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

Attercopus fimbriunguis, from 386 million years ago in the Devonian period, bears the earliest known silk-producing spigots, and was therefore hailed as a spider, but it lacked

spinnerets and hence was not a true spider. Several Carboniferous spiders were members of the Mesothelae, a primitive group now represented only by the Liphistiidae.

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

Relationships with other arthropods

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

Major sub-groups

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

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

The position of scorpions is particularly controversial. Some early fossils such as the Late Silurian *Proscorpius* have been classified by paleontologists as scorpions, but described as wholly aquatic as they had gills rather than book lungs or tracheae. Their mouths are

also completely under their heads and almost between the first pair of legs, as in the extinct eurypterids and living horseshoe crabs. This presents a difficult choice: classify *Proscorpius* and other aquatic fossils as something other than scorpions, despite the similarities; accept that "scorpions" are not monophyletic but consist of separate aquatic and terrestrial groups; or treat scorpions as more closely related to eurypterids and possibly horseshoe crabs than to spiders and other arachnids, so that either scorpions are not arachnids or "arachnids" are not monophyletic.

Diversity

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

Diversity of living chelicerates

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

Interaction with humans



A microscopic mite *Lorryia formosa*.

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

Cooked tarantula spiders are considered a delicacy in Cambodia, and by the Piaroa Indians of southern Venezuela. Spider venoms may be a less polluting alternative to

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

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

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

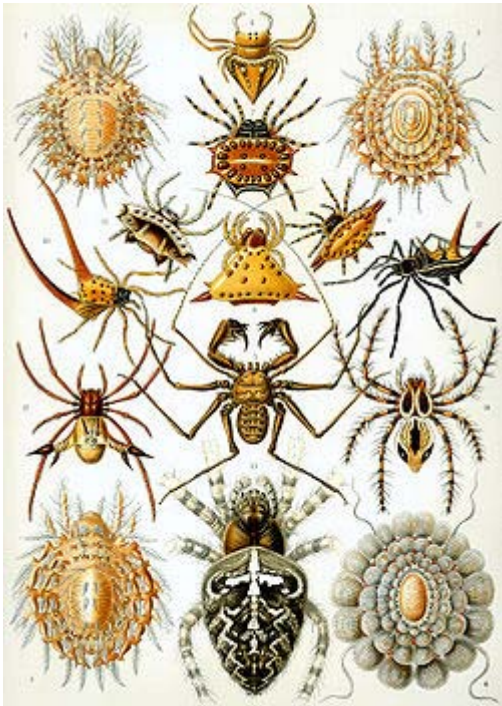
A few of the closely-related mites also infest humans, some causing intense itching by their bites and others by burrowing into the skin. Species that normally infest other animals such as rodents may infest humans if their normal hosts are eliminated. Three species of mite are a threat to honey bees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

Chapter 2

Arachnid

Arachnida

Temporal range: 420–0 Ma
Silurian to Recent



"Arachnida" from Ernst Haeckel's
Kunstformen der Natur, 1904

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Arachnida Cuvier, 1812

Orders

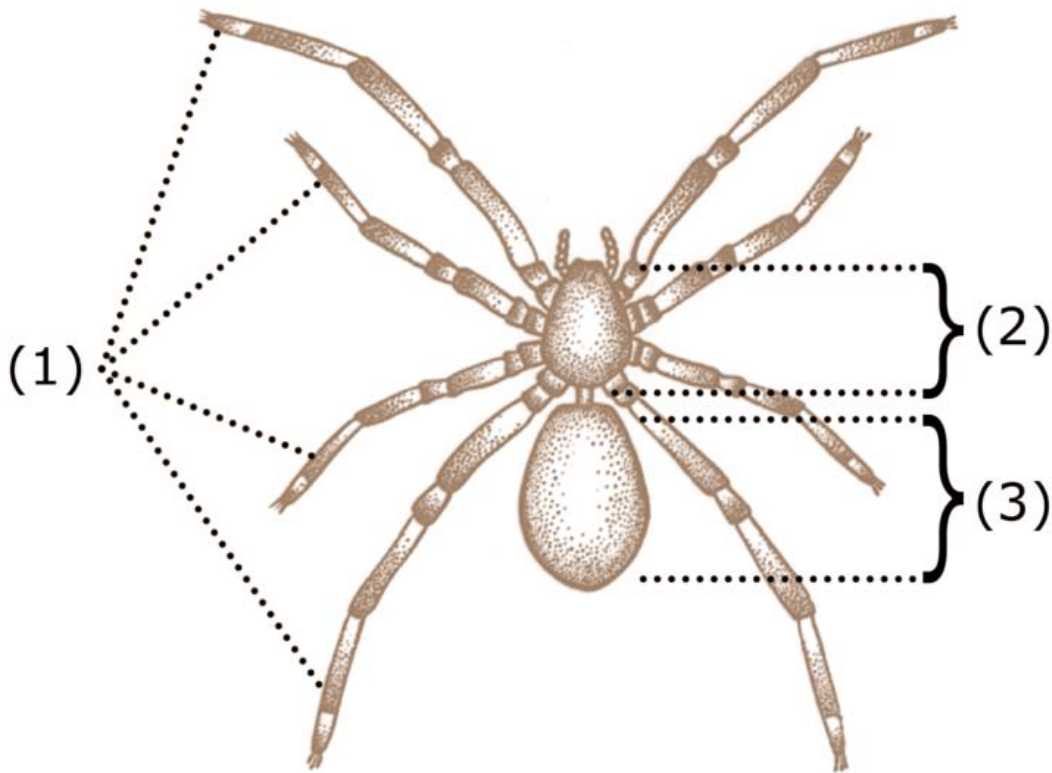
Acarina
Amblypygi

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

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

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

Anatomy



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

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

Arachnids are further distinguished from insects by the fact they have no antennae or wings. Their body is organized into two tagma called the prosoma, or cephalothorax, and the opisthosoma, or abdomen. The cephalothorax is derived from the fusion of the cephalon (head) and the thorax, and is usually covered by a single, unsegmented carapace. The abdomen is segmented in the more primitive forms, but varying degrees of fusion between the segments occur in many groups. It is typically divided into a

preabdomen and postabdomen, although this is only clearly visible in scorpions, and in some orders, such as the Acari, the abdominal sections are completely fused.

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

Physiology

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

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

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

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

Diet and digestive system

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

Arachnids pour digestive juices produced in their stomachs over their prey after killing it with their pedipalps and chelicerae. The digestive juices rapidly turn the prey into a broth of nutrients which the arachnid sucks into a pre-buccal cavity located immediately in

front of the mouth. Behind the mouth is a muscular, sclerotised pharynx, which acts as a pump, sucking the food through the mouth and on into the oesophagus and stomach. In some arachnids, the oesophagus also acts as an additional pump.

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

Senses

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

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

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

Reproduction

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

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

Systematics

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

- Araneae — true spiders (40,000 species)
 - Mesothelae — very rare, basal spiders, with abdomen segmented and spinnerets median
 - Opisthothelae — spiders with abdomen unsegmented and spinnerets located posteriorly
 - Araneomorphae — most common spiders
 - Mygalomorphae — tarantulas and tarantula-like spiders
- † Phalangiotarbida — extinct
- Opiliones — phalangids, harvestmen or daddy-long-legs (6,300 species)
 - Palpigradi — microwhip scorpions (80 species)
 - Pseudoscorpionida — pseudoscorpions (3,000 species)
 - Ricinulei — ricinuleids, hooded tickspiders (60 species)
 - Schizomida — "split middle" whip scorpions with divided exoskeletons (220 species)
 - Scorpiones — scorpions (2,000 species)
 - Solifugae — solpugids, windscorpions, sun spiders or camel spiders (900 species)
 - † Haptopoda — extinct
 - Thelyphonida — vinegaroons 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 — holothyran, 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 circumcapitular 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 Eriophyoidea) 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 (Tetranychidae), earth mites (Pentaleidae), 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 Holarachaeidae, and in the suborder Mesothelae (together about 350 species) can inject venom to protect themselves or to kill and liquefy prey. Only about 200 species, however, have bites that can pose

health problems to humans. Many larger species' bites may be painful, but will not produce lasting health concerns.

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

Haptopoda

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

Opiliones



Paroligolophus agrestis

Opiliones (formerly *Phalangida*, and better known as "**harvestmen**" or "**daddy longlegs**") are arachnids that are harmless to people and are known for their exceptionally long walking legs, compared to their body size. As of 2007, over 6,400 species of Phalangids have been discovered worldwide. The order Opiliones is divided into four suborders: Cyphophthalmi, Eupnoi, Dyspnoi and Laniatores. Well-preserved fossils have been found in the 410-million year old Rhynie cherts of Scotland; they look surprisingly

modern, suggesting that the basic structure of the harvestmen has not changed much since then.

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

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

Palpigradi

Palpigradi, commonly known as "microwhip scorpions", are tiny cousins of the uropygid, or whip scorpion, no more than 3 mm in length. They have a thin, pale, segmented carapace that terminates in a whip-like flagellum, made up of 15 segments. The carapace is divided into two plates between the third and fourth leg set. They have no eyes. Some species have three pairs of book lungs, while others have no respiratory organs at all. Approximately 80 species of Palpigradi have been described worldwide, in the families Eukoenediidae and Prokoenediidae, 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 phalangiotarbid 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 Megoperkulata 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 ($\frac{1}{12}$ to $\frac{1}{3}$ 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

Ricinulei (*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 3

Spider

Spiders

Temporal range: 319–0 Ma
Late Carboniferous to Recent



An Orb-weaver spider, Family: *Araneidae*

Scientific classification

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Chelicerata
(unranked): Arachnomorpha
Class: Arachnida
Order: **Araneae**
Clerck, 1757

Suborders

Mesothelae
Mygalomorphae
Araneomorphae

Diversity

109 families, c.40,000 species

Spiders (order **Araneae**) are air-breathing arthropods that have eight legs, and chelicerae with fangs that inject venom. They are the largest order of arachnids and rank seventh in total species diversity among all other groups of organisms. Spiders are found worldwide on every continent except for Antarctica, and have become established in nearly every habitat with the exception of air and sea colonization. As of 2008, approximately 40,000 spider species, and 109 families have been recorded by taxonomists; however, there has been confusion within the scientific community as to how all these families should be classified, as evidenced by the over 20 different classifications that have been proposed since 1900.

Anatomically, spiders differ from other arthropods in that the usual body segments are fused into two tagmata, the cephalothorax and abdomen, and joined by a small, cylindrical pedicel. Unlike insects, spiders do not have antennae. In all except the most primitive group, the Mesothelae, spiders have the most centralized nervous systems of all arthropods, as all their ganglia are fused into one mass in the cephalothorax. Unlike most arthropods, spiders have no extensor muscles in their limbs and instead extend them by hydraulic pressure.

Their abdomens bear appendages that have been modified into spinnerets that extrude silk from up to six types of silk glands within their abdomen. Spider webs vary widely in size, shape and the amount of sticky thread used. It now appears that the spiral orb web may be one of the earliest forms, and spiders that produce tangled cobwebs are more abundant and diverse than orb-web spiders. Spider-like arachnids with silk-producing spigots appear in the Devonian period about 386 million years ago, but these animals apparently lacked spinnerets. True spiders have been found in Carboniferous rocks from 318 to 299 million years ago, and are very similar to the most primitive surviving order, the Mesothelae. The main groups of modern spiders, Mygalomorphae and Araneomorphae, first appear in the Triassic period, before 200 million years ago.

A vegetarian species was described in 2008, but all other known species are predators, mostly preying on insects and on other spiders, although a few large species also take birds and lizards. Spiders use a wide range of strategies to capture prey: trapping it in sticky webs, lassoing it with sticky bolas, mimicking the prey to avoid detection, or running it down. Most detect prey mainly by sensing vibrations, but the active hunters have acute vision, and hunters of the genus *Portia* show signs of intelligence in their choice of tactics and ability to develop new ones. Spiders' guts are too narrow to take solids, and they liquidize their food by flooding it with digestive enzymes and grinding it with the bases of their pedipalps, as they do not have true jaws.

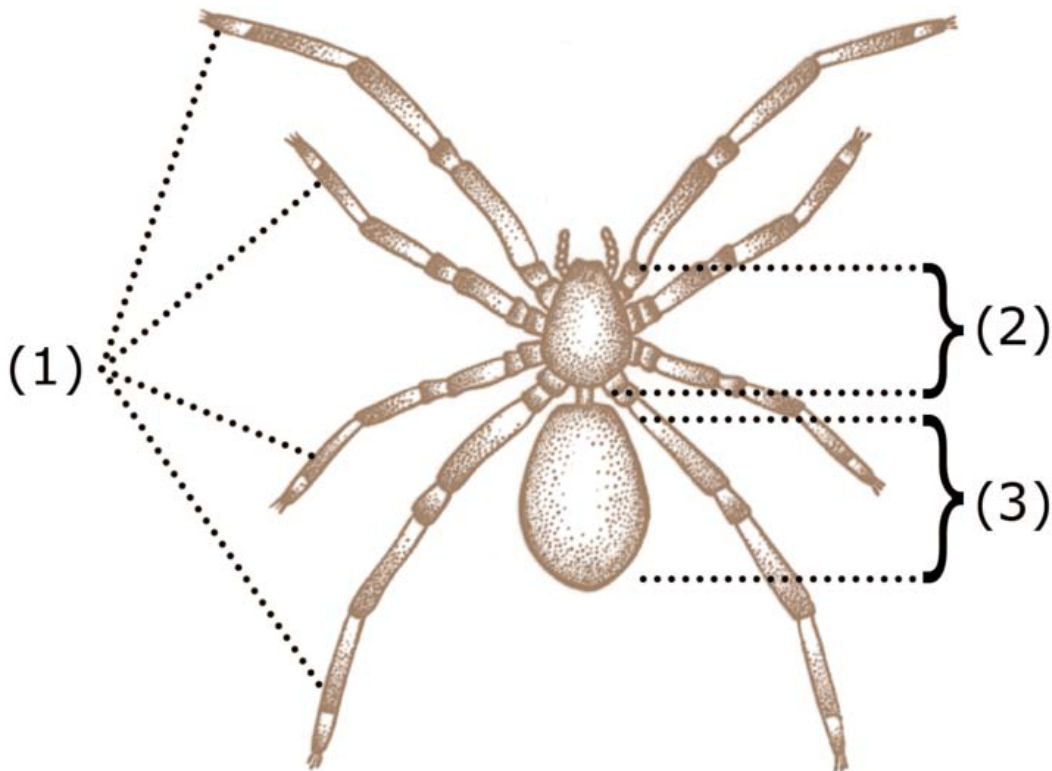
Male spiders identify themselves by a variety of complex courtship rituals to avoid being eaten by the females. Males of most species survive a few matings, limited mainly by their short life spans. Females weave silk egg-cases, each of which may contain hundreds of eggs. Females of many species care for their young, for example by carrying them around or by sharing food with them. A minority of species are social, building communal webs that may house anywhere from a few to 50,000 individuals. Social behavior ranges from precarious toleration, as in the aggressive widow spiders, to co-

operative hunting and food-sharing. Although most spiders live for at most two years, tarantulas and other mygalomorph spiders can live up to 25 years in captivity.

While the venom of a few species is dangerous to humans, scientists are now researching the use of spider venom in medicine and as non-polluting pesticides. Spider silk provides a combination of lightness, strength and elasticity that is superior to that of synthetic materials, and spider silk genes have been inserted into mammals and plants to see if these can be used as silk factories. As a result of their wide range of behaviors, spiders have become common symbols in art and mythology symbolizing various combinations of patience, cruelty and creative powers.

Description

Body plan



Arachnid anatomy:

- (1) four pairs of legs
- (2) cephalothorax
- (3) opisthosoma (abdomen)

Spiders are chelicerates and therefore arthropods. As arthropods they have: segmented bodies with jointed limbs, all covered in a cuticle made of chitin and proteins; heads that

are composed of several segments that fuse during the development of the embryo. Being chelicerates, their bodies consist of two tagmata, sets of segments that serve similar functions: the foremost one, called the cephalothorax or prosoma, is a complete fusion of the segments that in an insect would form two separate tagmata, the head and thorax; the rear tagma is called the abdomen or opisthosoma. In spiders the cephalothorax and abdomen are connected by a small cylindrical section, the pedicel. The pattern of segment fusion that forms chelicerates' heads is unique among arthropods, and what would normally be the first head segment disappears at an early stage of development, so that chelicerates lack the antennae typical of most arthropods. In fact chelicerates' only appendages ahead of the mouth are a pair of chelicerae, and they lack anything that would function directly as "jaws". The first appendages behind the mouth are called pedipalps, and serve different functions within different groups of chelicerates.



Phidippus audax, jumping spider: The basal parts of the chelicerae are the two iridescent green mouthparts.

Spiders and scorpions are members of one chelicerate group, the arachnids. Scorpions' chelicerae have three sections and are used in feeding. Spiders' chelicerae have two sections and terminate in fangs that are generally venomous, and fold away behind the upper sections while not in use. The upper sections generally have thick "beards" that filter solid lumps out of their food, as spiders can take only liquid food. Scorpions' pedipalps generally form large claws for capturing prey, while those of spiders are fairly small appendages whose bases also act as an extension of the mouth; in addition those of male spiders have enlarged last sections used for sperm transfer.

In spiders the cephalothorax and abdomen are joined by a small, cylindrical pedicel, which enables the abdomen to move independently when producing silk. The upper surface of the cephalothorax is covered by a single, convex carapace while the underside is covered by two rather flat plates. The abdomen is soft and egg-shaped. It shows no sign of segmentation, except that the primitive Mesothelae, whose living members are the Liphistiidae, have segmented plates on the upper surface.

Circulation and respiration

Like other arthropods, spiders are coelomates in which the coelom is reduced to small areas round 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. The heart is a tube in the upper part of the body, with a few ostia that act as non-return valves allowing blood to enter the heart from the hemocoel but prevent it from leaving before it reaches the front end. However in spiders it occupies only the upper part of the abdomen, and blood is discharged into the hemocoel by one artery that opens at the rear end of the abdomen and by branching arteries that pass through the pedicle and open into several parts of the cephalothorax. Hence spiders have open circulatory systems. The blood of many spiders that have book lungs contains the respiratory pigment hemocyanin to make oxygen transport more efficient.

Spiders have developed several different respiratory anatomies, based on book lungs, a tracheal system, or both. Mygalomorph and Mesothelae spiders have two pairs of book lungs filled with haemolymph, where openings on the ventral surface of the abdomen allow air to enter and diffuse oxygen. This is also the case for some basal araneomorph spiders like the family Hypochilidae, but the remaining members of this group have just the anterior pair of book lungs intact while the posterior pair of breathing organs are partly or fully modified into tracheae, through which oxygen is diffused into the haemolymph or directly to the tissue and organs. The trachea system has most likely evolved in small ancestors to help resist desiccation. The trachea were originally connected to the surroundings through a pair of openings called spiracles, but in the majority of spiders this pair of spiracles has fused into a single one in the middle, and moved backwards close to the spinnerets. Spiders that have tracheae generally have higher metabolic rates and better water conservation.

Feeding, digestion and excretion



A spider's fang

Uniquely among chelicerates, the final sections of spiders' chelicerae are fangs, and the great majority of spiders can use them to inject venom into prey from venom glands in the roots of the chelicerae. Like most arachnids including scorpions, spiders have a narrow gut that can only cope with liquid food and spiders have two sets of filters to keep solids out. They use one of two different systems of external digestion. Some pump digestive enzymes from the midgut into the prey and then suck the liquified tissues of the prey into the gut, eventually leaving behind the empty husk of the prey. Others grind the prey to pulp using the chelicerae and the bases of the pedipalps, while flooding it with enzymes; in these species the chelicerae and the bases of the pedipalps form a preoral cavity that holds the food they are processing.

The stomach in the cephalothorax acts as a pump that sends the food deeper into the digestive system. The mid gut bears many digestive ceca, compartments with no other exit, that extract nutrients from the food; most are in the abdomen, which is dominated by the digestive system, but a few are found in the cephalothorax.

Most spiders convert nitrogenous waste products into uric acid, which can be excreted as a dry material. Malpighian tubules ("little tubes") extract these wastes from the blood in the hemocoel and dump them into the cloacal chamber, from which they are expelled through the anus. Production of uric acid and its removal via Malpighian tubules are a water-conserving feature that has evolved independently in several arthropod lineages that can live far away from water, for example the tubules of insects and arachnids develop from completely different parts of the embryo. However a few primitive spiders, the sub-order Mesothelae and infra-order Mygalomorphae, retain the ancestral arthropod nephridia ("little kidneys"), which use large amounts of water to excrete nitrogenous waste products as ammonia.

Central nervous system

The basic arthropod central nervous system consists of a pair of nerve cords running below the gut, with paired ganglia as local control centers in all segments; a brain formed by fusion of the ganglia for the head segments ahead of and behind the mouth, so that the esophagus is encircled by this conglomeration of ganglia. Except for the primitive Mesothelae, of which the Liphistiidae are the sole surviving family, spiders have the much more centralized nervous system that is typical of arachnids: *all* the ganglia of all segments behind the esophagus are fused, so that the cephalothorax is largely filled with

nervous tissue and there are no ganglia in the abdomen; in the Mesothelae, the ganglia of the abdomen and the rear part of the cephalothorax remain unfused.

Sense organs

Eyes



This jumping spider's main ocelli (center pair) are very acute. The outer pair are "secondary eyes" and there are other pairs of secondary eyes on the sides and top of its head.

Most spiders have four pairs of eyes on the top-front area of the cephalothorax, arranged in patterns that vary from one family to another. The pair at the front are of the type called pigment-cup ocelli ("little eyes"), which in most arthropods 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 at the front of spiders' heads are pigment-cup ocelli that are capable of forming images. The other eyes are thought to be derived from the compound eyes of the ancestral chelicerates, but no longer have the separate facets typical of compound eyes. Unlike the main eyes, in many spiders these secondary eyes detect light reflected from a reflective tapetum lucidum, and wolf spiders can be spotted by torch light reflected from the tapeta. On the other hand jumping spiders' secondary eyes have no tapeta. Jumping spiders' visual acuity exceeds by a factor of ten that of dragonflies, which have by far the best vision among insects; in fact the human eye is only about five times sharper than a jumping spider's. They achieve this by a telephoto-

like series of lenses, a four-layer retina and the ability to swivel their eyes and integrate images from different stages in the scan. The downside is that the scanning and integrating processes are relatively slow.

Other senses

As with other arthropods, spiders' cuticles would block out information about the outside world, except that they are penetrated by many sensors or connections from sensors to the nervous system. In fact spiders and other arthropods have modified their cuticles into elaborate arrays of sensors. Various touch sensors, mostly bristles called setae, respond to different levels of force, from strong contact to very weak air currents. Chemical sensors provide equivalents of taste and smell, often by means of setae. Spiders also have in the joints of their limbs slit sensillae that detect forces and vibrations. In web-building spiders all these mechanical and chemical sensors are more important than the eyes, while the eyes are most important to spiders that hunt actively.

Like most arthropods, spiders lack balance and acceleration sensors and rely on their eyes to tell them which way is up. Arthropods' proprioceptors, sensors that report the force exerted by muscles and the degree of bending in the body and joints, are well understood. On the other hand little is known about what other internal sensors spiders or other arthropods may have.

Locomotion

Although all arthropods use muscles attached to the inside of the exoskeleton to flex their limbs, spiders and a few other groups still use hydraulic pressure to extend them, a system inherited from their pre-arthropod ancestors. As a result a spider with a punctured cephalothorax cannot extend its legs, and the legs of dead spiders curl up. Spiders can generate pressures up to eight times their resting level to extend their legs, and jumping spiders can jump up to 50 times their own length by suddenly increasing the blood pressure in the third or fourth pair of legs.

Most spiders that hunt actively, rather than relying on webs, have dense tufts of fine hairs between the paired claws at the tips of their legs. These tufts, known as scopulae, consist of bristles whose ends are split into as many as 1,000 branches, and enable spiders with scopulae to walk up vertical glass and upside down on ceilings. It appears that scopulae get their grip from contact with extremely thin layers of water on surfaces. Spiders, like most other arachnids, keep at least four legs on the surface while walking or running.

Silk production



An orb weaver producing silk from its spinnerets

The abdomen has no appendages except those that have been modified to form one to four (usually three) pairs of short, movable spinnerets, which emit silk. Each spinneret has many spigots, each of which is connected to one silk gland. There are at least six types of silk gland, each producing a different type of silk.

Silk is mainly composed of a protein very similar to that used in insect silk. It is initially a liquid, and hardens not by exposure to air but as a result of being drawn out, which changes the internal structure of the protein. It is similar in tensile strength to nylon and biological materials such as chitin, collagen and cellulose, but is much more elastic, in other words it can stretch much further before breaking or losing shape.

Some spiders have a cribellum, a modified spinneret with up to 40,000 spigots, each of which produces a single very fine fiber. The fibers are pulled out by the calamistrum, a comb-like set of bristles on the jointed tip of the cribellum, and combined into a composite woolly thread that is very effective in snagging the bristles of insects. The earliest spiders had cribella, which produced the first silk capable of capturing insects, before spiders developed silk coated with sticky droplets. However most modern groups of spiders have lost the cribellum.

Even species that do not build webs to catch prey use silk in several ways: as wrappers for sperm and for fertilized eggs; as a "safety rope"; for nest-building; and as "parachutes" by the young of some species.

Reproduction and life cycle



The tiny male of the Golden orb weaver (*Nephila clavipes*) (near the top of the leaf) is protected from the female by his producing the right vibrations in the web, and may be too small to be worth eating.

Spiders reproduce sexually and fertilization is internal but indirect, in other words the sperm is not inserted into the female's body by the male's genitals but by an intermediate stage. Unlike many land-living arthropods, male spiders do not produce ready-made spermatophores (packages of sperm) but spin small sperm webs on to which they ejaculate and then transfer the sperm to syringe-like structures on the tips of their pedipalps. When a male detects signs of a female nearby he checks whether she is of the same species and whether she is ready to mate; for example in species that produce webs or "safety ropes", the male can identify the species and sex of these objects by "smell".



Gasteracantha mammosa spiderlings next to their eggs capsule



Wolf spider carrying its young in its egg sac.

Spiders generally use elaborate courtship rituals to prevent the large females from eating the small males before fertilization, except where the male is so much smaller that he is not worth eating. In web-weaving species precise patterns of vibrations in the web are a major part of the rituals, while patterns of touches on the female's body are important in many spiders that hunt actively, and may "hypnotize" the female. Gestures and dances by the male are important for jumping spiders, which have excellent eyesight. If courtship is successful, the male injects his sperm from the pedipalps into the female's genital opening, known as the *epigyne*, on the underside of her abdomen. Female's reproductive tracts vary from simple tubes to systems that include seminal receptacles in which females store sperm and release it when they are ready.

Males of the genus *Tidarren* amputate one of their palps before maturation and enter adult life with one palp only. The palps are 20% of male's body mass in this species, and detaching one of the two improves mobility. In the Yemeni species *Tidarren argo*, the remaining palp is then torn off by the female. The separated palp remains attached to the female's epigynum for about four hours and apparently continues to function independently. In the meantime the female feeds on the palplless male. In over 60% of cases the female of the Australian redback spider kills and eats the male after it inserts its second palp into the female's genital opening; in fact the males co-operate by trying to impale themselves on the females' fangs. Observation shows that most male redbacks never get an opportunity to mate, and the "lucky" ones increase the likely number of offspring by ensuring that the females are well-fed. However males of most species

survive a few matings, limited mainly by their short life spans. Some even live for a while in their mates' webs.

Females lay up to 3,000 eggs in one or more silk egg sacs, which maintain a fairly constant humidity level. In some species the females die afterwards, but females of other species protect the sacs by attaching them to their webs, hiding them in nests, carrying them in the chelicerae or attaching them to the spinnerets and dragging them along.

Baby spiders pass all their larval stages inside the egg and hatch as spiderlings, very small and sexually immature but similar in shape to adults. Some spiders care for their young, for example a wolf spider's brood cling to rough bristles on the mother's back, and females of some species respond to the "begging" behaviour of their young by giving them their prey, provided it is no longer struggling, or even regurgitate food.

Like other arthropods, spiders have to molt to grow as their cuticle ("skin") cannot stretch. In some species males mate with newly molted females, which are too weak to be dangerous to the males. Most spiders live for only one to two years, although some tarantulas can live in captivity for over 20 years.



Goliath birdeater (*Theraphosa blondi*), the largest spider, next to a ruler.

Size

Spiders occur in a large range of sizes. The smallest, *Patu digua* from Colombia, are less than 0.37 mm (0.015 in) in body length. The largest and heaviest spiders occur among tarantulas, which can have body lengths up to 90 mm (3.5 in) and leg spans up to 250 mm (10 in).

Coloration

Only three classes of pigment (ommochromes, bilins and guanine) have been identified in spiders, although other pigments have been detected but not yet characterized. Melanins, carotenoids and pterins, very common in other animals, are apparently absent. In some species the exocuticle of the legs and prosoma is modified by a tanning process, resulting in brown coloration. Bilins are found, for example, in *Micrommata virescens*, resulting in its green color. Guanine is responsible for the white markings of the European garden spider *Araneus diadematus*. It is in many species accumulated in specialized cells called guanocytes. In genera such as *Tetragnatha*, *Leucauge*, *Argyrodes* or *Theridiosoma*, guanine creates their silvery appearance. While guanine is originally an end-product of protein metabolism, its excretion can be blocked in spiders, leading to an increase in its storage. Structural colors occur in some species, which are the result of the diffraction, scattering or interference of light, for example by modified setae or scales. The white prosoma of *Argiope* results from hairs reflecting the light, *Lycosa* and *Josa* both have areas of modified cuticle that act as light reflectors.

Ecology and behavior

Non-predatory feeding

Although spiders are generally regarded as predatory, the jumping spider *Bagheera kiplingi* gets over 90% of its food from fairly solid plant material produced by acacias as part of a mutually beneficial relationship with a species of ant.

Juveniles of some spiders in the families Anyphaenidae, Corinnidae, Clubionidae, Thomisidae and Salticidae feed on plant nectar. Laboratory studies show that they do so deliberately and over extended periods, and periodically clean themselves while feeding. These spiders also prefer sugar solutions to plain water, which indicates that they are seeking nutrients. Since many spiders are nocturnal, the extent of nectar consumption by spiders may have been under-estimated. Nectar contains amino acids, lipids, vitamins and minerals in addition to sugars, and studies have shown that other spider species live longer when nectar is available. Feeding on nectar avoids the risks of struggles with prey, and the costs of producing venom and digestive enzymes.

Various species are known to feed on dead arthropods (scavenging), web silk, and their own shed exoskeletons. Pollen caught in webs may also be eaten, and studies have shown that young spiders have a better chance of survival if they have the opportunity to eat

pollen. In captivity, several spider species are also known to feed on bananas, marmalade, milk, egg yolk and sausages.

Methods of capturing prey



The *P. graeffei* or leaf-curling spider's web serves both as a trap and as a way of making its home in a leaf.

The best-known method of prey capture is by means of sticky webs. Varying placement of webs allows different species of spider to trap different insects in the same area, for example flat horizontal webs trap insects that fly up from vegetation underneath while flat vertical webs trap insects in horizontal flight. Web-building spiders have poor vision, but are extremely sensitive to vibrations.

Females of the water spider *Argyroneta aquatica* build underwater "diving bell" webs which they fill with air and use for digesting prey, molting, mating and raising offspring. They live almost entirely within the bells, darting out to catch prey animals that touch the bell or the threads that anchor it. A few spiders use the surfaces of lakes and ponds as "webs", detecting trapped insects by the vibrations that these cause while struggling.

Net-casting spiders weave only small webs but then manipulate them to trap prey. Those of the genus *Hyptiotes* and the family Theridiosomatidae stretch their webs and then release them when prey strike them, but do not actively move their webs. Those of the family Deinopidae weave even smaller webs, hold them outstretched between their first two pairs of legs, and lunge and push the webs as much as twice their own body length to trap prey, and this move may increase the webs' area by a factor of up to ten. Experiments have shown that *Deinopis spinosus* has two different techniques for trapping prey: backwards strikes to catch flying insects, whose vibrations it detects; and forward strikes to catch ground-walking prey that it sees. These two techniques have also been observed in other deinopids. Walking insects form most of the prey of most deinopids, but one population of *Deinopis subrufus* appears to live mainly on tipulid flies that they catch with the backwards strike.

Mature female bolas spiders of the genus *Mastophora* build "webs" that consist of only a single "trapeze line", which they patrol. They also construct a bolas made of a single thread, tipped with a large ball of very wet sticky silk. They emit chemicals that resemble the pheromones of moths, and then swing the bolas at the moths. Although they miss on about 50% of strikes, they catch about the same weight of insects per night as web-weaving spiders of similar size. The spiders eat the bolas if they have not made a kill in about 30 minutes, rest for a while, and then make new bolas. Juveniles and adult males are much smaller and do not make bolas. Instead they release different pheromones that attract moth flies, and catch them with their front pairs of legs.



Trapdoor spider (family: Ctenizidae), an ambush predator.

The primitive Liphistiidae, the "trapdoor spiders" (family Ctenizidae) and many tarantulas are ambush predators that lurk in burrows, often closed by trapdoors and often surrounded by networks of silk threads that alert these spiders to the presence of prey. Other ambush predators do without such aids, including many crab spiders, and a few species that prey on bees, which see ultraviolet, can adjust their ultraviolet reflectance to match the flowers in which they are lurking. Wolf spiders, jumping spiders, fishing spiders and some crab spiders capture prey by chasing it, and rely mainly on vision to locate prey.



Portia uses both webs and cunning, versatile tactics to overcome prey.

Some jumping spiders of the genus *Portia* hunt other spiders in ways that seem intelligent, outflanking their victims or luring them from their webs. Laboratory studies show that *Portia's* instinctive tactics are only starting points for a trial-and-error approach from which these spiders learn very quickly how to overcome new prey species. However they seem to be relatively slow "thinkers", which is not surprising, as their brains are vastly smaller than those of mammalian predators.



An ant-mimicking jumping spider

Ant-mimicking spiders face several challenges: they generally develop slimmer abdomens and false "waists" in the cephalothorax to mimic the three distinct regions (tagmata) of an ant's body; they wave the first pair of legs in form to their heads to mimic antennae, which spiders lack, and to conceal the fact that they have eight legs rather than six; they develop large color patches round one pair of eyes to disguise the fact that they generally have eight simple eyes, while ants have two compound eyes; they cover their bodies with reflective hairs to resemble the shiny bodies of ants. In some spider species, males and females mimic different ant species, as female spiders are usually much larger than males. Ant-mimicking spiders also modify their behavior to resemble that of the target species of ant; for example, many adopt a zig-zag pattern of movement, ant-mimicking jumping spiders avoid jumping, and spiders of the genus *Synemosyna* walk on the outer edges of leaves in the same way as *Pseudomyrmex*. Ant-mimicry in many spiders and other arthropods may be for protection from predators that hunt by sight, including birds, lizards and spiders. However, several ant-mimicking spiders prey either on ants or on the ants' "livestock", such as aphids. When at rest, the ant-mimicking crab spider *Amyciaea* does not closely resemble *Oecophylla*, but while hunting it imitates the behavior of a dying ant to attract worker ants. After a kill, some ant-mimicking spiders hold their victims between themselves and large groups of ants to avoid being attacked.

Defense



Threat display by a Sydney funnel-web spider (*Atrax robustus*).

There is strong evidence that spiders' coloration is camouflage that helps them to evade their major predators, birds and parasitic wasps, both of which have good color vision. Many spider species are colored so as to merge with their most common backgrounds, and some have disruptive coloration, stripes and blotches that break up their outlines. In a few species, such as the Hawaiian happy-face spider, *Theridion grallator*, several coloration schemes are present in a ratio that appears to remain constant, and this may make it more difficult for predators to recognize the species. Most spiders are insufficiently dangerous or unpleasant-tasting for warning coloration to offer much benefit. However a few species with powerful venoms, large jaws or irritant hairs have patches of warning colors, and some actively display these colors when threatened.

Many of the family Theraphosidae, which includes tarantulas and baboon spiders, have urticating hairs on their abdomens and use their legs to flick them at attackers. These hairs are fine setae (bristles) with fragile bases and a row of barbs on the tip. The barbs cause intense irritation but there is no evidence that they carry any kind of venom. A few defend themselves against wasps by including networks of very robust threads in their webs, giving the spider time to flee while the wasps are struggling with the obstacles. The golden wheeling spider, *Carparachne aureoflava*, of the Namibian desert escapes parasitic wasps by flipping onto its side and cartwheeling down sand dunes.

Social spiders

A few species of spiders that build webs live together in large colonies and show social behavior, although not as complex as in social insects. *Anelosimus eximius* (in the family Theridiidae) can form colonies of up to 50,000 individuals. The genus *Anelosimus* has a strong tendency towards sociality: all known American species are social, and species in Madagascar are at least somewhat social. Members of other species in the same family but several different genera have independently developed social behavior. For example, although *Theridion nigroannulatum* belongs to a genus with no other social species, *T. nigroannulatum* build colonies that may contain several thousand individuals that cooperate in prey capture and share food. Other communal spiders include several *Philoponella* species (family Uloboridae), *Agelena consociata* (family Agelenidae) and *Mallos gregalis* (family Dictynidae). Social predatory spiders need to defend their prey against kleptoparasites ("thieves"), and larger colonies are more successful in this. The herbivorous spider *Bagheera kiplingi* lives in small colonies which help to protect eggs and spiderlings. Even widow spiders (genus *Latrodectus*), which are notoriously aggressive and cannibalistic, have formed small colonies in captivity, sharing webs and feeding together.

Web types

There is no consistent relationship between the classification of spiders and the types of web they build: species in the same genera may build very similar or significantly different webs. Nor is there much correspondence between spiders' classification and the chemical composition of their silks. Convergent evolution in web construction, in other words use of similar techniques by remotely related species, is "rampant". Non-orb web

designs and the spinning behaviors that produce them have received very little attention from arachnologists, despite the fact that the majority of spiders build non-orb webs. The basic radial-then-spiral sequence visible in orb webs and the "sense of direction" required to build them may have been inherited from the common ancestors of most spider groups. It used to be thought that the sticky orb web was an evolutionary innovation resulting in the diversification of the Orbiculariae. Now, however, it appears that non-orb spiders are a sub-group that evolved from orb-web spiders, and non-orb spiders have over 40% more species and are four times as abundant as orb-web spiders. Their greater success may be because sphecid wasps, which are often the dominant predators on spiders, much prefer to attack spiders that have flat webs.

Orb webs



Nephila clavata, a golden orb weaver

About half the potential prey that hit orb webs escape. A web has to perform three functions: intercepting the prey (intersection); absorbing its momentum without breaking (stopping); and trapping the prey by entangling it or sticking to it (retention). No single design is best for all prey. For example: wider spacing of lines will increase the web's area and hence its ability to intercept prey, but reduce its stopping power and retention; closer spacing, larger sticky droplets and thicker lines would improve retention, but would make it easier for potential prey to see and avoid the web, at least during the day. However there are no consistent differences between orb webs built for use during the day and those built for use at night. In fact there is no simple relationship between orb web design features and the prey they capture, as each orb-weaving species takes a wide range of prey.

The hubs of orb webs, where the spiders lurk, are usually above the center as the spiders can move downwards faster than upwards. If there is an obvious direction in which the spider can retreat to avoid its own predators, the hub is usually offset towards that direction.

Horizontal orb webs are fairly common, despite being less effective at intercepting and retaining prey and more vulnerable to damage by rain and falling debris. Various researchers have suggested that horizontal webs offer compensating advantages, such as: reduced vulnerability to wind damage; reduced visibility to prey flying upwards, because of the back-lighting from the sky; enabling oscillations to catch insects in slow horizontal flight. However there is no single explanation for the common use of horizontal orb webs.

Spiders often attach highly visible silk bands called decorations or stabilimenta to their webs. Field research suggests that webs with more decorative bands captured more prey per hour. However a laboratory study showed that spiders reduce the building of these decorations if they sense the presence of predators.

There are several unusual variants of orb web, many of them convergently evolved, including: attachment of lines to the surface of water, possibly to trap insects in or on the surface; webs with twigs through their centers, possibly to hide the spiders from predators; "ladder-like" webs that appear most effective in catching moths. However the significance of many variations is unclear.

In 1973, Skylab 3 took two orb-web spiders into space to test their web-spinning capabilities in zero gravity. At first both produced rather sloppy webs, but they adapted quickly.

Tangleweb / cobweb spiders



A funnel web.

Members of the family Theridiidae weave irregular, tangled, three-dimensional webs, popularly known as cobwebs. There seems to be an evolutionary trend towards a reduction in the amount of sticky silk used, leading to its total absence in some species. The construction of cobwebs is less stereotyped than that of orb-webs, and may take several days.

Other types of webs

The Linyphiidae generally make horizontal but uneven sheets, with tangles of stopping threads above. Insects that hit the stopping threads fall on to the sheet or are shaken on to it by the spider, and are held by sticky threads on the sheet until the spider can attack from below.

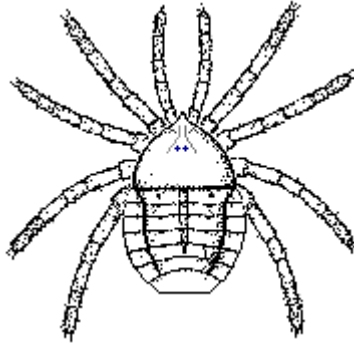
Evolution

Fossil record



Spider preserved in amber

Although the fossil record of spiders is considered poor, almost 1000 species have been described from fossils. Because spiders' bodies are quite soft, the vast majority of fossil spiders have been found preserved in amber. The oldest known amber that contains fossil arthropods dates from 130 million years ago in the Early Cretaceous period. In addition to preserving spiders' anatomy in very fine detail, pieces of amber show spiders mating, killing prey, producing silk and possibly caring for their young. In a few cases amber has preserved spiders' egg sacs and webs, occasionally with prey attached; the oldest fossil web found so far is 100 million years old. Earlier spider fossils come from a few lagerstätten, places where conditions were exceptionally suited to preserving fairly soft tissues.



Palaeotarbus jerami, a trigonotarbid and the oldest known arachnid

The oldest known arachnid is the trigonotarbid *Palaeotarbus jerami*, from about 420 million years ago in the Silurian period, and had a triangular cephalothorax and segmented abdomen, as well as eight legs and a pair of pedipalps. *Attercopus fimbriunguis*, from 386 million years ago in the Devonian period, bears the earliest known silk-producing spigots, and was therefore hailed as a spider. However these spigots may have been mounted on the underside of the abdomen rather than on spinnerets, which are modified appendages and whose mobility is important in the building of webs. Hence *Attercopus* and the similar Permian arachnid *Permarachne* may not have been true spiders, and probably used silk for lining nests or producing egg-cases rather than for building webs.

Several Carboniferous spiders were members of the Mesothelae, a primitive group now represented only by the Liphistiidae. The mesothelid *Paleothele montceauensis*, from the Late Carboniferous over 299 million years ago, had five spinnerets. Although the Permian period 299 to 251 million years ago saw rapid diversification of flying insects, there are very few fossil spiders from this period.

The main groups of modern spiders, Mygalomorphae and Araneomorphae, first appear in the Triassic well before 200 million years ago. Some Triassic mygalomorphs appear to be members of the family Hexathelidae, whose modern members include the notorious Sydney funnel-web spider, and their spinnerets appear adapted for building funnel-shaped webs to catch jumping insects. Araneomorphae account for the great majority of modern spiders, including those that weave the familiar orb-shaped webs. The Jurassic and Cretaceous periods provide a large number of fossil spiders, including representatives of many modern families.

Family tree

It is now agreed that spiders (Araneae) are monophyletic (i.e., members of a group of organisms which form a clade, consisting of a last common ancestor and all of its descendants). There has been debate about what their closest evolutionary relatives are, and how all of these evolved from the ancestral chelicerates, which were marine animals. The cladogram on the right is based on J.W. Shultz' analysis (2007). Other views include proposals that: scorpions are more closely related to the extinct marine scorpion-like

eurypterids than to spiders; spiders and Amblypygi are a monophyletic group. The appearance of several multi-way branchings in the tree on the right shows that there are still uncertainties about relationships between the groups involved.

Arachnids lack some features of other chelicerates, including backward-pointing mouths and gnathobases ("jaw bases") at the bases of their legs; both of these features are part of the ancestral arthropod feeding system. Instead they have mouths that point forwards and downwards, and all have some means of breathing air. Spiders (Araneae) are distinguished from other arachnid groups by several characteristics, including spinnerets and, in males, pedipalps that are specially adapted for sperm transfer.

Taxonomy

Spiders are divided into two sub-orders, Mesothelae and Opisthothelae, of which the latter contains two infra-orders, Mygalomorphae and Araneomorphae. Over 40,000 living species of spiders (order Araneae) have been identified and are currently grouped into about 110 families and about 3,700 genera by arachnologists.

Sub-order	Spider diversity			Features		Spinnerets	Striking direction of fangs
	Species	Genera	Families	Segmented plates on top of abdomen	Ganglia in abdomen		
Mesothelae	87	5	1	Yes	Yes	Four pairs, in some species one pair fused, under middle of abdomen	Downwards and forwards
Mygalomorphae	2,600	300	15	No, but yes in some fossils	No	One, two or three pairs under rear of abdomen	From sides to center, like pincers
Araneomorphae	37,000	3,400	93				

Mesothelae



Ryuthela secundaria, a member of the Liphistiidae

The only living members of the primitive Mesothelae are the family Liphistiidae, found only in Southeast Asia, China, and Japan. Most of the Liphistiidae construct silk-lined burrows with thin trapdoors, although some species of the genus *Liphistius* build camouflaged silk tubes with a second trapdoor as an emergency exit. Members of the genus *Liphistius* run silk "tripwires" outwards from their tunnels to help them detect approaching prey, while those of genus *Heptathela* do not and instead rely on their built-in vibration sensors. Spiders of the genus *Heptathela* have no venom glands although they do have venom gland outlets on the fang tip.

The extinct families Arthrolycosidae, found in Carboniferous and Permian rocks, and Arthromygalidae, so far found only in Carboniferous rocks, have been classified as members of the Mesothelae.

Mygalomorphae



A Mexican red-kneed tarantula *Brachypelma smithi*

The Mygalomorphae, which first appeared in the Triassic period, are generally heavily built and hairy, with large, robust chelicerae and fangs. Well-known examples include tarantulas, trapdoor spiders and the Australasian funnel-web spiders. Most spend the majority of their time in burrows, and some run silk tripwires out from these, but a few build webs to capture prey. However mygalomorphs cannot produce the piriform silk that the Araneomorphae use as instant adhesive to glue silk to surfaces or to other strands of silk, and this makes web construction more difficult for mygalomorphs. Since mygalomorphs rarely "balloon" by using air currents for transport, their populations often form clumps. In addition to arthropods, mygalomorphs prey on frogs and lizards, and snails.

Araneomorphae

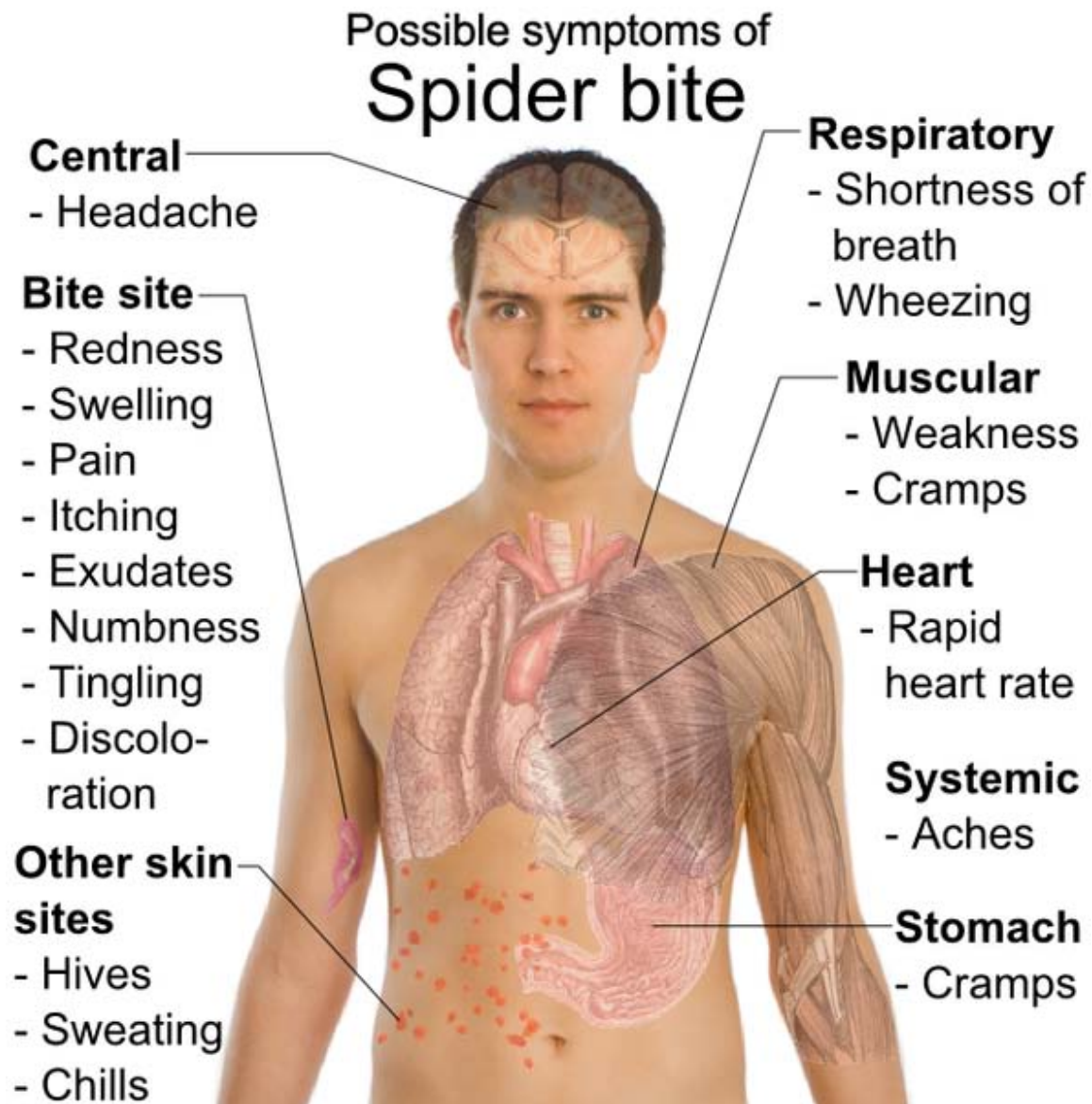


The pincer-like fangs of a *Cheiracanthium punctorium*

In addition to accounting for over 90% of spider species, the Araneomorphae, also known as the "true spiders", include orb-web spiders, the cursorial wolf spiders, and jumping spiders, as well as the only known herbivorous spider, *Bagheera kiplingi*.

Spiders and people

Spider bites



Symptoms that are most common in toxic spider bites

Most spiders will only bite humans in self-defense, and few produce worse effects than a mosquito bite or bee-sting. Most of those with medically serious bites, such as recluse spiders and widow spiders, are shy and bite only when they feel threatened, although this can easily arise by accident. Funnel web spiders' defensive tactics are aggressive and their venom, although they rarely inject much, has resulted in 13 known human deaths. On the other hand the Brazilian wandering spider requires very little provocation.

There were about 100 reliably reported deaths from spider bites in the 20th century, but about 1,500 from jellyfish stings. Many alleged cases of spider bites may represent incorrect diagnoses, which would make it more difficult to check the effectiveness of treatments for genuine bites.

Benefits to humans



Cooked tarantula spiders are considered a delicacy in Cambodia.

Cooked tarantula spiders are considered a delicacy in Cambodia, and by the Piaroa Indians of southern Venezuela – provided the highly irritant hairs, the spiders' main defense system, are removed first.

Spider venoms may be a less polluting alternative to conventional pesticides as they are deadly to insects but the great majority are harmless to vertebrates. Australian funnel web spiders are a promising source as most of the world's insect pests have had no opportunity to develop any immunity to their venom, and funnel web spiders thrive in captivity and are easy to "milk". It may be possible to target specific pests by engineering genes for the production of spider toxins into viruses that infect species such as cotton bollworms.

Possible medical uses for spider venoms are being investigated, for the treatment of cardiac arrhythmia, Alzheimer's disease, strokes, and erectile dysfunction.

Because spider silk is both light and very strong, attempts are being made to produce it in goats' milk and in the leaves of plants, by means of genetic engineering.

Arachnophobia

Arachnophobia is a specific phobia, an abnormal fear of spiders or anything reminiscent of spiders, such as webs or spider-like shapes. It is one of the most common specific phobias, and some statistics show that 50 percent of women and 10 percent of men show symptoms.

It may be an exaggerated form of an instinctive response that helped early humans to survive, or perhaps a cultural phenomenon that is most common in predominantly European societies.

Spiders in symbolism and culture



This Moche ceramic depicts a spider, and dates from around 300 CE.

Spiders have been the focus of fears, stories and mythologies of various cultures for centuries. They have symbolized patience due to their hunting technique of setting webs and waiting for prey, as well as mischief and malice for the painful death their venom causes.

Web-spinning also caused the association of the spider with creation myths as they seem to have the ability to produce their own worlds. The Moche people of ancient Peru worshipped nature. They placed emphasis on animals and often depicted spiders in their art.

Chapter 4

Scorpion

Scorpion

Temporal range: Silurian–Recent



Asian forest scorpion in Khao Yai National Park, Thailand

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Arachnida
Subclass:	Dromopoda
Order:	Scorpiones C. L. Koch, 1837

Superfamilies

Buthoidea
Chaeriloidea
Chactoidea
Changster
Iuroidea
Scorpionoidea

Scorpions are predatory arthropod animals of the order **Scorpiones** within the class Arachnida. They have eight legs and are easily recognized by the pair of grasping claws and the narrow, segmented tail, carried in a characteristic forward curve over the back, ending with a venomous stinger.

Scorpions are found widely distributed over all continents, except Antarctica, in a variety of terrestrial habitats except the high latitude tundra. Scorpions number about 1752 described species, with thirteen extant families recognised to date. The taxonomy has undergone changes and is likely to change further, as a number of genetic studies are bringing forth new information.

Though the scorpion has a fearsome reputation as venomous, only 25 species have venom capable of killing a human being.

Etymology

The word *scorpion* is thought to have originated in Middle English between 1175 and 1225 AD from Old French *skorpiō*, itself derived from the Latin word *scorpion*, which in turn has its roots in the Greek word σκορπίος – *skorpíos*.

Geographical distribution

Scorpions are found on all major land masses except Antarctica. Scorpions did not occur naturally in Great Britain, New Zealand and some of the islands in Oceania, but have now been accidentally introduced in some of these places by human trade and commerce. The greatest diversity of scorpions in the Northern Hemisphere is to be found in the subtropical areas lying between latitudes 23° N and 38° N. Above these latitudes, the diversity decreases, with the northernmost occurrence of scorpions being the northern scorpion *Paruroctonus boreus* at 50° N.

Scorpions are found in virtually every habitat, including high elevation mountain-tops, caves and intertidal zones, with the exception of boreal ecosystems such as the tundra, high-altitude taiga and the permanently snow-clad tops of some mountains. As regards microhabitats, scorpions may be ground-dwelling, tree-living, lithophilic (rock-loving) or psammophilic (sand-loving); some species such as *Vaejovis janssi* are versatile and found in every type of habitat in Baja California while others occupy specialised niches such as *Euscorpius carpathicus* which occupies the littoral zone of the shore.

Five colonies of scorpions (*Euscorprius flavicaudis*) have established themselves in Sheerness on the Isle of Sheppey in the United Kingdom. This small population has been resident since the 1860s, having probably arrived with imported fruit from Africa. This scorpion species is small and completely harmless to humans. This marks the northernmost limit in the world where scorpions live in the wild.

Classification

There are thirteen families and about 1,400 described species and subspecies of scorpions. In addition, there are 111 described taxa of extinct scorpions.

This classification is based on that of Soleglad & Fet (2003), which replaced the older, unpublished classification of Stockwell. Additional taxonomic changes are from papers by Soleglad et al. (2005).

Systematics

The following classification covers extant taxa to the rank of family.

Order Scorpiones

Infraorder Orthosterni Pocock, 1911

- Parvorder Pseudochactida Soleglad et Fet, 2003
 - Superfamily Pseudochactoidea Gromov, 1998
 - Family Pseudochactidae Gromov, 1998
- Parvorder Buthida Soleglad et Fet, 2003
 - Superfamily Buthoidea C. L. Koch, 1837
 - Family Buthidae C. L. Koch, 1837 (thick-tailed scorpions)
 - Family Microcharmidae Lourenço, 1996
- Parvorder Chaerilida Soleglad et Fet, 2003
 - Superfamily Chaeriloidea Pocock, 1893
 - Family Chaerilidae Pocock, 1893
- Parvorder Iurida Soleglad et Fet, 2003
 - Superfamily Chactoidea Pocock, 1893
 - Family Chactidae Pocock, 1893
 - Family Euscorpiidae Laurie, 1896
 - Family Superstitioniidae Stahnke, 1940
 - Family Vaejovidae Thorell, 1876
 - Superfamily Iuroidea Thorell, 1876
 - Family Caraboctonidae Kraepelin, 1905 (hairy scorpions)
 - • Family Iuridae Thorell, 1876

- Superfamily Scorpionoidea Latreille, 1802
 - Family Bothriuridae Simon, 1880
 - Family Hemiscorpiidae Pocock, 1893 (= Ischnuridae, =Liochelidae) (rock scorpions, creeping scorpions, or tree scorpions)
 - Family Scorpionidae Latreille, 1802 (burrowing scorpions or pale-legged scorpions)

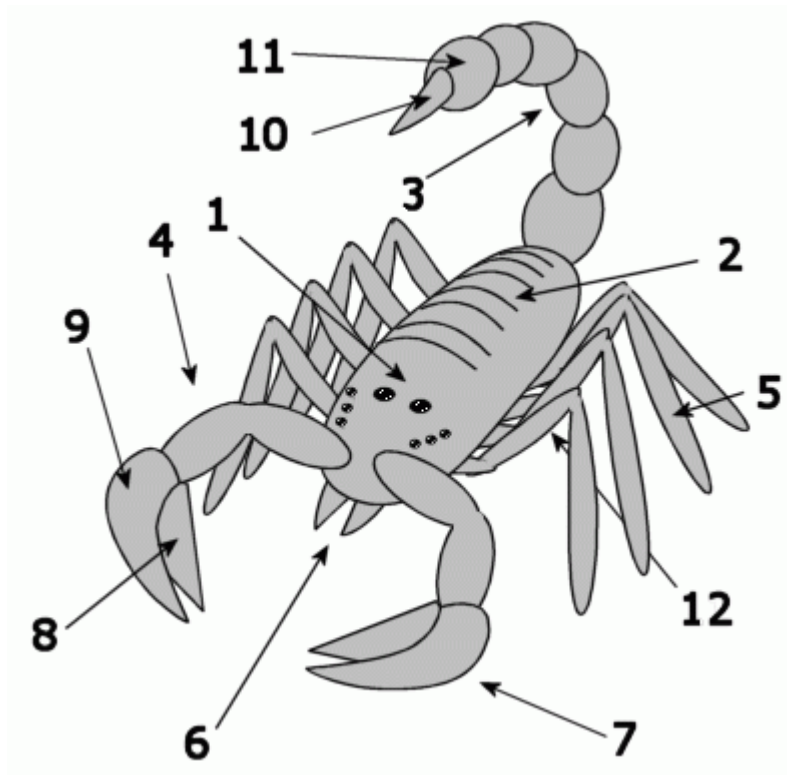
Fossil record

Scorpions have been found in many fossil records, including marine Silurian deposits, coal deposits from the Carboniferous Period and in amber. The oldest known scorpions lived around 430 million years ago in the Silurian period, on the bottom of shallow tropical seas. These first scorpions had gills instead of the present forms' book lungs. Currently, 111 fossil species of scorpion are known. Unusually for arachnids, there are more species of Palaeozoic scorpion than Mesozoic or Cenozoic ones.

The *eurypterids*, marine creatures which lived during the Paleozoic era, share several physical traits with scorpions and may be closely related to them. Various species of Eurypterida could grow to be anywhere from 10 to 25 centimetres (3.9 to 9.8 in) in length. However, they exhibit anatomical differences marking them off as a group distinct from their Carboniferous and Recent relatives. Despite this, they are commonly referred to as "sea scorpions". Their legs are thought to have been short, thick, tapering and to have ended in a single strong claw; it appears that they were well-adapted for maintaining a secure hold upon rocks or seaweed against the wash of waves, like the legs of a shore crab.

Biology

Anatomy



Scorpion anatomy:

1 = Cephalothorax or *Prosoma*;

2 = Abdomen or *Mesosoma*;

3 = Tail or *Metasoma*;

4 = Claws or *Pedipalps*

5 = Legs;

6 = Mouth parts or *Chelicerae*;

7 = pincers or *Chelae*;

8 = Moveable claw or *Tarsus*;

9 = Fixed claw or *Manus*;

10 = Sting or *Telson*;

11 = Anus.



Barb of an Arizona bark scorpion

The body of a scorpion is divided into three parts (tagmata): the head (cephalothorax), the abdomen (mesosoma) and the tail (metasoma).

Cephalothorax

The cephalothorax, also called the *prosoma*, is the scorpion's "head", comprising the carapace, eyes, chelicerae (mouth parts), pedipalps (commonly called claws, pincers or chelae) and four pairs of walking legs. The scorpion's exoskeleton is thick and durable, providing good protection from predators. Scorpions have two eyes on the top of the head, and usually two to five pairs of eyes along the front corners of the head. The position of the eyes on the head depends in part on the hardness or softness of the soil upon which they spend their lives.

The pedipalp is a segmented, chelate (clawed) appendage used for prey immobilization, defense, and sensory purposes. The segments of the pedipalp (from closest to the body outwards) are coxa, trochanter, femur (humerus), patella, tibia (tarsus, hand or movable claw) and manus (fixed claw). A scorpion has darkened or granular raised linear ridges, called "keels" or *carinae* on the pedipalp segments and on other parts of the body which are useful taxonomically.

Mesosoma

The abdomen, also called the *opisthosoma*, consists of seven segments (somites), each covered dorsally by a sclerotized plate (tergum) and also ventrally for segments 3 to 7. The first abdominal segment bears a pair of genital opercula which cover the gonopore. Segment 2 consists of the basal plate with the pectines. Each of the mesosomal segments 3 to 7 have a pair of spiracles which are the openings for the scorpion's respiratory organs, known as book lungs. The spiracle openings may be slits, circular, elliptical, or oval.

Metasoma

The metasoma, the scorpion's tail, comprises five caudal segments (the first tail segment looks like a last mesosoman segment), 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.

On rare occasions, scorpions can be born with two metasomata (tails). Two-tailed scorpions are not a different species, merely a genetic abnormality.

Fluorescence in ultraviolet light



A scorpion under a black light. In normal lighting, this scorpion appears black.

Scorpions are also known to glow when exposed to certain wavelengths of ultraviolet light such as that produced by a blacklight, due to the presence of fluorescent chemicals in the cuticle. One fluorescent component is now known to be beta-carboline. A hand-held UV lamp has long been a standard tool for nocturnal field surveys of these animals. Fluorescence occurs as a result of sclerotization and increases in intensity with each successive instar.

Life and habits

Scorpions have quite variable lifespans and the actual 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 species *Hadrurus arizonensis*). Lifespan of *Hadogenes* species in the wild is estimated at 25–30 years.

Scorpions prefer to live in areas where the temperatures range from 20 °C to 37 °C (68 °F to 99 °F), but may survive from freezing temperatures to the desert heat. Scorpions of the genus *Scorpiops* living in high Asian mountains, bothriurid scorpions from Patagonia and small *Euscorprius* scorpions from Central Europe can all survive winter temperatures of about –25 °C (–13 °F). In Repetek (Turkmenistan), there live seven species of scorpions (of which *Pectinibuthus birulai* is endemic) in temperatures which vary from –31 °C to 50 °C.

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 exhibit photophobic behavior, primarily to evade detection by their predators such as birds, centipedes, lizards, mice, possums, and rats.

Scorpions are opportunistic predators of small arthropods and insects, although the larger kinds have been known to kill small lizards and mice. The large pincers are studded with highly sensitive tactile hairs, and the moment an insect touches these, they use their chelae (pincers) to catch the prey. 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. This will kill or paralyze the prey so the scorpion can eat it. Scorpions have a relatively unique style of eating using chelicerae, small claw-like structures that protrude from the mouth that are unique to the Chelicerata among arthropods. The chelicerae, which are very sharp, are used to pull small amounts of food off the prey item for digestion into a *pre-oral cavity* below the chelicerae and carapace. Scorpions can only ingest food in a liquid form; they have external digestion. The digestive juices from the gut are egested onto the food and the digested food sucked in liquid form. Any solid indigestible matter (fur, exoskeleton, etc.) is trapped by setae in the pre-oral cavity, which is ejected by the scorpion.

Scorpions can consume huge amounts of food at one sitting. They have a very efficient food storage organ and a very low metabolic rate combined with a relatively inactive lifestyle. This enables scorpions to survive long periods when deprived of food; some are

able to survive 6 to 12 months of starvation. Scorpions excrete very little; their waste consists mostly of insoluble nitrogenous waste such as xanthine, guanine and uric acid.

Reproduction

Most scorpions reproduce sexually, and most species have male and female individuals. However, some species, such as *Hottentotta hottentotta*, *Hottentotta caboverdensis*, *Liocheles australasiae*, *Tityus columbianus*, *Tityus metuendus*, *Tityus serrulatus*, *Tityus stigmurus*, *Tityus trivittatus*, and *Tityus uruguayensis*, reproduce through parthenogenesis, a process in which unfertilised eggs develop into living embryos. Parthenogenic reproduction starts following the scorpion's final moult to maturity and continues thereafter.

Sexual reproduction is accomplished by the transfer of a spermatophore from the male to the female; scorpions possess a complex courtship and mating ritual to effect this transfer. Mating starts with the male and female locating and identifying each other using a mixture of pheromones and vibrational communication. Once they have satisfied the other that they are of opposite sex and of the correct species, mating can commence.

The courtship starts with the male grasping the female's pedipalps with his own; the pair then perform a "dance" called the "*promenade à deux*". In reality this is the male leading the female around searching for a suitable place to deposit his spermatophore. The courtship ritual can involve several other behaviours such as juddering and a cheliceral kiss, in which the male's chelicerae – clawlike mouthparts – grasp the female's in a smaller more intimate version of the male's grasping the female's pedipalps and in some cases injecting a small amount of his venom into her pedipalp or on the edge of her cephalothorax, probably as a means of pacifying the female.

When the male has identified a suitable location, he deposits the spermatophore and then guides the female over it. This allows the spermatophore to enter her genital opercula, which triggers release of the sperm, thus fertilizing the female. The mating process can take from 1 to 25+ hours and depends on the ability of the male to find a suitable place to deposit his spermatophore. If mating goes on for too long, the female may eventually lose interest, breaking off the process.

Once the mating is complete, the male and female will separate. The male will generally retreat quickly, most likely to avoid being cannibalised by the female, although sexual cannibalism is infrequent with scorpions.

Birth and development



Compsobuthus weneri female with young

Unlike the majority of arachnid 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 molt. Before the first molt, scorplings cannot survive naturally without the mother, since they depend on her for protection and to regulate their moisture levels. Especially in species which display more advanced sociability (e.g. *Pandinus* spp.), the young/mother association can continue for an extended period of time. The size of the litter depends on the species and environmental factors, and can range from two to over a hundred scorplings. The average litter however, consists of around 8 scorplings.

The young generally resemble their parents. Growth is accomplished by periodic shedding of the exoskeleton (ecdysis). A scorpion's developmental progress is measured in instars (how many moults it has undergone). Scorpions typically require between five and seven moults to reach maturity. Moulting commences with a split in the old exoskeleton just below the edge of the carapace (at the front of the prosoma). The scorpion then emerges from this split; the pedipalps and legs are first removed from the old exoskeleton, followed eventually by the metasoma. When it emerges, the scorpion's new exoskeleton is soft, making the scorpion highly vulnerable to attack. The scorpion must constantly stretch while the new exoskeleton hardens to ensure that it can move when the hardening is complete. The process of hardening is called sclerotization. The

new exoskeleton does not fluoresce; as sclerotization occurs, the fluorescence gradually returns.

Relationship with humans

Scorpion sting and venom

All known scorpion species possess venom and use it primarily to kill or paralyze their prey so that it can be eaten; in general it is fast-acting, allowing for effective prey capture. It is also used as a defense against predators. The venom is a mixture of compounds (neurotoxins, enzyme inhibitors, etc.) each not only causing a different effect, but possibly also targeting a specific animal. Each compound is made and stored in a pair of glandular sacs and is released in a quantity regulated by the scorpion itself. Of the 1000+ known species of scorpion, only 25 have venom that is dangerous to humans; all belong to the family Buthidae.

First aid

First aid for scorpion stings is generally symptomatic. It includes strong analgesia, either systemic (opiates or paracetamol) or locally applied (such as a cold compress). Hypertensive crises are treated with anxiolytics and vasodilators.

Medical use



The deathstalker has powerful venom.

The key ingredient of the venom is a scorpion toxin protein.

Short chain scorpion toxins constitute the largest group of potassium (K^+) channel blocking peptides; an important physiological role of the KCNA3 channel, also known as $K_v1.3$, is to help maintain large electrical gradients for the sustained transport of ions such as Ca^{2+} that controls T lymphocyte (T cell) proliferation. Thus $K_v1.3$ blockers could be potential immunosuppressants for the treatment of autoimmune disorders (such as rheumatoid arthritis, inflammatory bowel disease and multiple sclerosis).

The venom of *Uroplectes lineatus* is clinically important in dermatology.

Toxins being investigated include:

- Chlorotoxin is a 36-amino acid peptide found in the venom of the deathstalker scorpion (*Leiurus quinquestriatus*) which blocks small-conductance chloride channels. The fact that chlorotoxin binds preferentially to glioma cells has allowed the development of new methods, that still are under investigation, for the treatment and diagnosis of several types of cancer.

- Maurotoxin from the venom of the Tunisian *Scorpio maurus palmatus*

Consumption



Eating scorpions in Beijing, China



Scorpion and snake wine

Fried scorpion is a traditional dish from Shangdong, China.

As a part of Chinese medicine, scorpion wine and snake wine are used as analgesic and antidote.

Chapter 5

Opiliones

Opiliones

Temporal range: 400–0 Ma
Devonian - Recent



A male *Phalangium opilio*, showing the long legs

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Arachnida
Subclass:	Dromopoda
Order:	Opiliones Sundevall, 1833

Suborders

- Cyphophthalmi
- Eupnoi
- Dyspnoi
- Laniatores

Diversity

4 suborders, > 6,400 species

Opiliones (formerly *Phalangida*) are an order of arachnids commonly known as **harvestmen**. As of 2006, over 6,400 species of harvestmen have been discovered worldwide, although the real number of extant species may exceed 10,000. The order Opiliones can be divided into four suborders: Cyphophthalmi, Eupnoi, Dyspnoi and Laniatores. Well-preserved fossils have been found in the 400-million year old Rhynie cherts of Scotland, which look surprisingly modern, indicating that the basic structure of the harvestmen has not changed much since then. Phylogenetic position is disputed: their closest relatives may be the mites (Acari) or the Novogenuata (the Scorpiones, Pseudoscorpiones and Solifugae).

Although they belong to the class of arachnids, harvestmen are not spiders, which are of the order Araneae rather than the order Opiliones.

In some places, harvestmen are known by the name "**daddy longlegs**" or "**granddaddy longlegs**", but this name is also used for two other unrelated arthropods: the crane fly (Tipulidae) and the cellar spider (Pholcidae).

Physical description



Hadrobunus grandis

These arachnids are known for their exceptionally long walking legs, compared to body size, although there are also short-legged species. The difference between harvestmen

and spiders is that in harvestmen the two main body sections (the abdomen with ten segments and cephalothorax, or *prosoma* and *opisthosoma*) are broadly joined, so that they appear to be one oval structure; they also have no venom or silk glands. 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 most posterior abdominal segments can be reduced or separated in the middle on the surface to form two plates lying next to each other. The second pair of legs are longer than the others and work as antennae. This can be hard to see in short-legged species.

The feeding apparatus (stomotheca) differs from other arachnids in that ingestion is not restricted to liquid, but chunks of food can be taken in. The stomotheca is formed by extensions from the pedipalps and the first pair of legs.

They have a single pair of eyes in the middle of their heads, oriented sideways. However, there are eyeless species, such as the Brazilian *Caecobunus termitarum* (Grassatores) from termite nests, *Giupponia chagasi* (Gonyleptidae) from caves, and all species of Guasiniidae.



A harvestman (a male *Phalangium opilio*), showing the almost fused arrangement of abdomen and cephalothorax that distinguishes these arachnids from spiders.

Harvestmen have a pair of prosomatic defensive scent glands (ozopores) that secrete a peculiar smelling fluid when disturbed, confirmed in some species to contain noxious quinones. Harvestmen do not have silk glands and do not possess venom glands, posing absolutely no danger to humans (see below). They do not have book lungs, and breathe through tracheae only. Between the base of the fourth pair of legs and the abdomen a pair of spiracles are located, 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 the copulation is direct as the male has a penis (while the female has an ovipositor). All species lay eggs.

The legs continue to twitch after they are detached. This is because there are 'pacemakers' located in the ends of the first long segment (femur) of their legs. These pacemakers send signals via the nerves to the muscles to extend the leg and then the leg relaxes between signals. While some harvestman's legs will twitch for a minute, other kinds have been recorded to twitch for up to an hour. The twitching has been hypothesized as a means to keep the attention of a predator while the harvestman escapes.

Typical body length does not exceed 7 millimetres (0.28 in), with some species smaller than one mm, although the largest species *Trogulus torosus* (*Trogulidae*) can reach a length of 22 millimetres (0.87 in). However, leg span is much larger and can exceed 160 millimetres (6.3 in). Most species live for a year.

Behavior



Harvestman eating a skink tail

Many species are omnivorous, eating primarily small insects and all kinds of plant material and fungi; some are scavengers, feeding upon dead organisms, bird dung and other fecal material. This broad range is quite unusual in arachnids, which are usually pure predators. Most hunting harvestmen ambush their prey, although active hunting is also found. Because their eyes cannot form images, they use their second pair of legs as antennae to explore their environment. Unlike most other arachnids, harvestmen do not have a sucking stomach or a filtering mechanism. Rather, they ingest small particles of their food, thus making them vulnerable to internal parasites such as gregarines.

Although parthenogenetic species do occur, most harvestmen reproduce sexually. Mating involves direct copulation, rather than the deposition of a spermatophore. The males of some species offer a secretion from their chelicerae to the female before copulation. Sometimes the male guards the female after copulation and, in many species, the males defend territories. The females lay eggs shortly after mating or anytime up to several months later. Some species build nests for this purpose. A unique feature of harvestmen is that in some species the male is solely responsible for guarding the eggs resulting from multiple partners, often against egg-eating females, and subjecting the eggs to regular cleaning. The eggs can hatch anytime after the first 20 days, up to almost half a year after being laid. Harvestmen need from four to eight nymphal stages to reach maturity, with six the most common.

They are mostly nocturnal and colored in hues of brown, although there are a number of diurnal species which have vivid patterns in yellow, green and black with varied reddish and blackish mottling and reticulation.

To deal with predators such as birds, mammals, amphibians and spiders, some species glue debris onto their body, while many play dead when disturbed. Many species can detach their legs, which keep on moving, to confuse predators. Especially long-legged species vibrate their body ("bobbing"), probably also to confuse predators. This is similar to the behavior of the similar looking but unrelated cellar spider, which vibrates wildly in its web when touched. Scent glands emit substances that can deter larger predators, but are also effective against ants.



Mites parasitising a harvestman

Many species of harvestmen easily tolerate members of their own species, with aggregations of many individuals often found at protected sites near water. These aggregations can count up to 200 animals in the Laniatores, but more than 70,000 in certain Eupnoi. This behavior is likely a strategy against climatic odds, but also against predators, combining the effect of scent secretions, and reducing the probability of each individual of being eaten.

Endangered status

All troglobitic species (of all animal taxa) are considered to be at least threatened in Brazil. There are four species of Opiliones in the Brazilian National List for endangered

species, all of them cave-dwelling species. *Giupponia chagasi*, *Iandumoema uai*, *Pachylospeleus strinatii* and *Spaeleoleptes spaeleus*.

Several Opiliones in Argentina appear to be vulnerable, if not endangered. These include *Pachyloidellus fulvigranulatus*, which is found only on top of Cerro Uritorco, the highest peak in the Sierras Chicas chain (provincia de Cordoba) and *Pachyloides borellii* is in rainforest patches in North West Argentina which are in an area being dramatically destroyed by humans. The cave living *Picunchenops spelaeus* is apparently endangered through human action. So far no harvestman has been included in any kind of a Red List in Argentina and therefore they receive no protection.

Maiorerus randoi has only been found in one cave in the Canary Islands. It is included in the Catálogo Nacional de especies amenazadas (National catalog of threatened species) from the Spanish government.

Texella reddelli and *Texella reyesi* are listed as endangered species in the USA. Both are from caves in central Texas. *Texella cokendolpheri* from a cave in central Texas and *Calicina minor*, *Microcina edgewoodensis*, *Microcina homi*, *Microcina jungi*, *Microcina leei*, *Microcina lumi*, and *Microcina tiburona* from around springs and other restricted habitats of central California are being considered for listing as endangered species, but as yet receive no protection.

Misconception



Uncate (tong-like) chelicerae typical of harvestmen (200x magnification); these appendages are analogous to a spider's fangs.

An urban legend claims that the harvestman is the most venomous animal in the world, but possesses fangs too short or a mouth too round and small to bite a human and therefore is not dangerous (the same myth applies to *Pholcus phalangioides* and the crane fly, which are both also called a 'daddy longlegs'). This is untrue on several counts. None of the known species of harvestmen has venom glands; their chelicerae are not hollowed fangs but grasping claws that are typically very small and definitely not strong enough to break human skin. This myth is so pervasive that it was debunked by two popular television shows, *MythBusters* and "Bill Nye The Science Guy".

Research

Harvestmen are a scientifically neglected group. Description of new taxa has always been dependent on the activity of a few dedicated taxonomists. Carl Friedrich Roewer

described about a third (2,260) of today's known species from the 1910s to the 1950s, and published the landmark systematic work *Die Weberknechte der Erde* (Harvestmen of the World) in 1923, with descriptions of all species known to that time. Other important taxonomists in this field include Eugène Simon, Tord Tamerlan Teodor Thorell, William Sørensen and Zac Jewell and also Heinrich VanStratunburgs around the turn of the 20th century, and later Cândido Firmino de Mello-Leitão and Reginald Frederick Lawrence. Since 1980, study of the biology and ecology of harvestmen has intensified, especially in South America.

Phylogeny

Harvestmen are very old arachnids. Fossils from the Devonian Rhynie chert, 410 million years ago, already show characteristics like tracheae and sexual organs, proving that the group has lived on land since that time. They are probably closely related to the scorpions, pseudoscorpions and solifuges; these four orders form the clade Dromopoda. The Opiliones have remained almost unchanged morphologically over a long period. Indeed, one species discovered in China, fossilized by fine grained volcanic ash around 165 million years ago, is hardly discernible from its modern day descendant and belongs to an existing family of harvestman.

Etymology

The Swedish naturalist and arachnologist Carl Jakob Sundevall (1801–1875) honored the naturalist Martin Lister (1638–1712) by adopting his term Opiliones for this order; Lister taxonomically described three species from England, United Kingdom.

Fossil record



A male *Phalangium opilio*, showing the long legs and the *tarsomeres* (the many small segments making up the end of each leg)

Despite their long history, few harvestman fossils are known. This is mainly due to their delicate body structure and terrestrial habitat, making it unlikely to be found in sediments. As a consequence, most known fossils have been preserved as amber.

The oldest known harvestman, from the 400 million years old Devonian Rhynie chert, already has almost all the characteristics of modern species, placing the origin of harvestmen in the Silurian, or even earlier.

Interestingly, no fossils of Cyphophthalmi or Laniatores much older than 50 million years are known, despite the former presenting a basal clade, and the latter having probably diverged from the Dyspnoi more than 300 million years ago.

Naturally, most finds are from comparatively recent times, but it is interesting that while there are more than 20 known species from the Cenozoic, and at least seven from the Paleozoic, only one species from the Mesozoic has yet been found.

Paleozoic

The 400 million years old *Eophalangium sheari* is known from two specimens, one a female, the other a male. The female bears an ovipositor and is about 10 millimetres (0.39 in) long, the male penis can be discerned too. It is not definitely known if both sexes belong to the same species. They have long legs, tracheae, and no median eyes.

Brigantibunum listoni from East Kirkton near Edinburgh in Scotland is almost 340 million years old. Its placement is rather uncertain, apart from it being a harvestman.

From about 300 million years ago (mya) there are several finds from the Coal Measures of North America and Europe. While the two described *Nemastomoides* species are currently grouped as Dyspnoi, they look more like Eupnoi.

Kustarachne tenuipes was shown in 2004 to be a harvestman, after residing for almost hundred years in its own arachnid order, the "Kustarachnida".

There are some fossils from the Permian that are possibly harvestmen, but these are not well preserved.

Described species

- *Eophalangium sheari* (Eupnoi) — Early Devonian (Rhynie, Scotland)
- *Brigantibunum listoni* (Eupnoi?)— Early Carboniferous (East Kirkton, Scotland)
- *Eotrogulus fayoli* Thevenin, 1901 (Dyspnoi: † Eotrogulidae) — Upper Carboniferous (Commentry, France)
- *Nemastomoides elaveris* Thevenin, 1901 (Dyspnoi: † Nemastomoididae) — Upper Carboniferous (Commentary, France)
- *Nemastomoides longipes* Petrunkevitch — Upper Carboniferous (Mazon Creek, USA)
- *Kustarachne tenuipes* Scudder, 1890 (Eupnoi?) — Upper Carboniferous (Mazon Creek, USA)
- *Echinopustulus samuelnelsoni* Dunlop, 2004 (Dyspnoi?) — Upper Carboniferous (Western Missouri, USA)

Mesozoic

No fossil harvestmen are known from the Triassic. They are also so far absent from the Lower Cretaceous Crato Formation of Brazil, which has yielded many other terrestrial arachnids. An unnamed long-legged harvestman was reported from the Early Cretaceous of Koonwarra, Victoria, Australia, which may be a Eupnoi.

Halitherses grimaldii from Burmese amber (c. 100 million years ago) is a long-legged Dyspnoi with large eyes, which may be related to the Ortholasmatinae (Nemastomatidae).

Cenozoic

Unless otherwise noted, all species are from the Eocene.

- *Trogulus longipes* Haupt, 1956 (Dyspnoi: Trogulidae) — Geiseltal, Germany
- *Philacarus hispaniolensis* (Laniatores: Samoidae?) — Dominican amber
- *Kimula* species (Laniatores: Kimulidae) — Dominican amber
- *Hummelinckiolus silhavyi* Cokendolpher & Poinar, 1998 (Laniatores: Samoidae) — Dominican amber
- *Caddo dentipalpis* (Eupnoi: Caddidae) — Baltic amber
- *Dicranopalpus ramiger* (Koch & Berendt, 1854) (Eupnoi: Phalangiidae) — Baltic amber
- *Opilio ovalis* (Eupnoi: Phalangiidae?) — Baltic amber
- *Cheiromachus coriaceus* Menge, 1854 (Eupnoi: Phalangiidae?) — Baltic amber
- *Leiobunum longipes* (Eupnoi: Sclerosomatidae) — Baltic amber
- *Histicostoma tuberculatum* (Dyspnoi: Nemastomatidae) — Baltic amber
- *Mitostoma denticulatum* (Dyspnoi: Nemastomatidae) — Baltic amber
- *Nemastoma incertum* (Dyspnoi: Nemastomatidae) — Baltic amber
- *Sabacon claviger* (Dyspnoi: Sabaconidae) — Baltic amber
- *Petrunkevitchiana oculata* (Petrunkevitch, 1922) (Eupnoi: Phalangioida) — Florissant, USA (Oligocene)
- *Proholoscotolemon nemastomoides* (Laniatores: Cladonychiidae) — Baltic amber
- *Siro platypedibus* (Cyphophthalmi: Sironidae) — Bitterfeld amber
- *Amauropilio atavus* (Cockerell, 1907) (Eupnoi: Sclerosomatidae) — Florissant, USA (Oligocene)
- *Amauropilio lacoiei* (*A. lawei*?) (Petrunkevitch, 1922) — Florissant, USA (Oligocene)
- *Pellobunus proavus* Cokendolpher, 1987 (Laniatores: Samoidae) — Dominican amber
- *Phalangium* species (Eupnoi: Phalangiidae) — near Rome, Italy (Quaternary)

Chapter 6

Acari

Acari

Temporal range: Early
Devonian–Recent



Peacock mite (*Tuckerella* sp.),
false-color SEM, magnified
260×

Scientific classification [e |

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Chelicerata
Class: Arachnida
Subclass: **Acari**
Leach, 1817

Superorders

Acariformes
Parasitiformes

Acari (or **Acarina**) are a taxon of arachnids that contains mites and ticks. The diversity of the Acari is extraordinary and its fossil history goes back to at least the early Devonian period. As a result, acarologists (the people who study mites and ticks) have proposed a complex set of taxonomic ranks to classify mites. In most modern treatments, the Acari is considered a subclass of Arachnida and is composed of 2-3 superorders or orders:

Acariformes (or Actinotrichida), Parasitiformes (or Anactinotrichida), and Opilioacariformes; the latter is often considered a subgroup within the Parasitiformes. The monophyly of the Acari is open to debate, and the relationships of the acarines to other arachnids is not at all clear. In older treatments, the subgroups of the Acarina were placed at order rank, but as their own subdivisions have become better-understood, it is more usual to treat them at superorder rank.

Most acarines are minute to small (e.g. 0.08–1.00 millimetre or 0.0031–0.039 inch), but the largest Acari (some ticks and red velvet mites) may reach lengths of 10–20 millimetres (0.39–0.79 in). 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** (from Greek ἄκαρι, *akari*, a type of mite; and -λογία, *-logia*), and the leading scientific journals for acarology include *Acarologia*, *Experimental and Applied Acarology* and the *International Journal of Acarology*.

Morphology

Mites are arachnids and, as such, should have a segmented body with the segments organised into two tagmata: a prosoma (cephalothorax) and an opisthosoma (abdomen). However, only the faintest traces of primary segmentation remain in mites, the prosoma and opisthosoma are insensibly fused, and a region of flexible cuticle (the circumcapitular furrow) separates the chelicerae and pedipalps from the rest of the body. This anterior body region is called the capitulum or gnathosoma and, according to some workers, is also found in 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* (family Eriophyidae) have a worm-like 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'.

The mouth parts of mites may be adapted for biting, stinging, sawing or sucking. They breath through tracheae, stigmata (small openings of the skin), intestines and the skin itself. Species hunting for other mites have very acute senses, but many mites are eyeless. The central eyes of arachnids are always missing, or they are fused into a single eye. Thus, any eye number from none to five may occur.

Ontogeny



A soft-bodied tick of the family Argasidae, beside eggs it has just laid

Acarine ontogeny typically consists of an egg, a prelarval stage (often absent), a larval stage (hexapod except in Eriophyoidea which have only two pairs of legs), and a series of nymphal stages. Any or all of these stages except the adult may be suppressed or occur only within the body of a previous stage. Larvae (and prelarvae) have a maximum of three pairs of legs (legs are often reduced to stubs or absent in prelarvae); legs IV are added at the first nymphal stage. Usually a maximum of three nymphal stages are present and they are referred to in sequence as protonymph, deutonymph, and tritonymph; however, some soft ticks have supernumerary nymphal stages. The females of some Tarsonemidae bear sexually mature young. If one or more nymphal stages are absent, then authors may disagree on which stages are present. Only the Oribatida pass through all developmental stages.

Diversity and lifestyles

Acarines are extremely diverse. They 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 predatory 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.

Economic importance

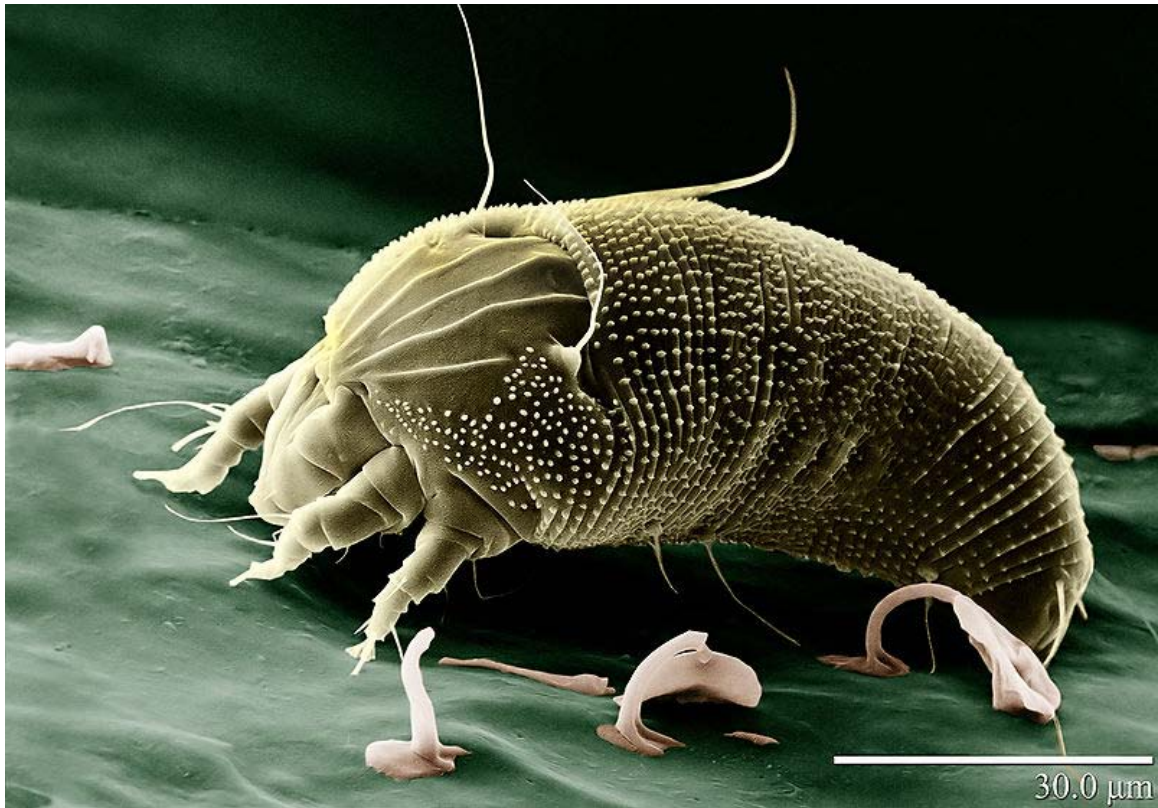
Damage to crops is perhaps the most costly economic effect of mites, especially by the spider mites and their relatives (Tetranychoidae), earth mites (Penthaeleidae), thread-footed mites (Tarsonemidae) and the gall and rust mites (Eriophyidae).

Some parasitic forms affect humans and other mammals, causing damage by their feeding, and can even be vectors of diseases such as scrub typhus, rickettsialpox, Lyme disease, Q fever, Colorado tick fever, tularemia, tick-borne relapsing fever, babesiosis, ehrlichiosis and tick-borne meningoencephalitis. A well known effect of mites on humans is their role as an allergen and the stimulation of asthma in people affected by respiratory disease.

The use of predatory mites (e.g. Phytoseiidae) in pest control and herbivorous mites that infest weeds are also of importance. An unquantified, but major positive contribution of the Acari is their normal functioning in ecosystems, especially their roles in the decomposer subsystem.

Chemical agents used to control ticks and mites include dusting sulfur and ivermectin.

Taxonomy



Rust mite, *Aceria anthocoptes* (size: 50 micrometres)



Male tick (size: 2 mm)

The phylogeny of the Acari is still disputed and several taxonomic schemes have been proposed for their classification. The third edition of the standard textbook *A Manual of Acarology* uses a system of six orders, grouped into two superorders:

- Superorder **Parasitiformes** – ticks and a variety of mites.
 - Opilioacarida – mites that superficially resemble harvestmen (Opiliones, hence their name)
 - Holothyrida
 - Ixodida – hard and soft ticks
 - Mesostigmata – bird mites, phytoseiid mites, *Raubmilben*
 - Sejoidea

- Trigynaspida
 - Monogynaspida
- Superorder **Acariformes** – the most diverse group of mites.
 - Trombidiformes – plant parasitic mites (spider mites, peacock mites, gall mites, red-legged earth mites, etc.), snout mites, chiggers, hair follicle mites, velvet mites, water mites, etc.
 - Sphaerolichida
 - Prostigmata
 - Sarcoptiformes
 - Endeostigmata – basal sarcoptiform lineages
 - Oribatida – oribatid mites, beetle mites, armored mites (also cryptostigmata)
 - Endeostigmata – stored product, fur, feather, dust, and human itch mites, etc.

Chapter 7

Pseudoscorpion

Pseudoscorpions

Temporal range: 380–0 Ma
Devonian to Recent



Scientific classification

Kingdom: Animalia
Phylum: Arthropoda
Class: Arachnida
Subclass: Dromopoda
Order: **Pseudoscorpionida**
Haeckel, 1866

Superfamilies

- Chthonioidea
- Neobisioidea
- Garypoidea
- Cheiridioidea
- Fealloidea
- Cheliferoidea

A **pseudoscorpion**, (also known as a *false scorpion* or *book scorpion*), is an arachnid belonging to the order **Pseudoscorpionida**, also known as Pseudoscorpiones or Chelonethida.

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.

Characteristics

Pseudoscorpions are small arachnids with a flat, pear-shaped body and pincers that resemble those of scorpions. They usually range from 2 to 8 millimetres (0.08 to 0.31 in) in length. The largest known species is *Garypus titanius* of Ascension Island at up to 12 mm (0.5 in).



Pseudoscorpion hitchhiking on a fly

The abdomen, known as the opisthosoma, is made up of twelve segments, each protected by plates (called tergites above and sternites below) made of chitin. The abdomen is short and rounded at the rear, rather than extending into a segmented tail and stinger like true scorpions (the fact that they look exactly like scorpions, aside from not having a stinger

tail, is the source of the name "Pseudoscorpion"). The color of the body can be yellowish-tan to dark-brown, with the paired claws often a contrasting color. They may have two, four or no eyes.

A pseudoscorpion has eight legs with five to seven segments; the number of fused segments is used to distinguish families and genera. They have two very long *palpal chelae* (pedipalps or pincers) which 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 immobilize 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. However, they do not have book lungs as most of their closest relatives, the spiders do. They breathe through spiracles, a trait they share with the insects.

Behavior

Some species have an elaborate mating dance, where the male 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 fertilized 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. Many species molt in a small, silken igloo that protects them from enemies during this vulnerable period. After reaching adulthood, pseudoscorpions live two to three years. They are active in the warm months of the year, overwintering in silken cocoons when the weather grows cold. Smaller species live in debris and humus. Some species are arboreal, i.e., live on trees. Some others are phagophiles. Some species are phoretic. They may sometimes be found feeding on mites under the wing covers of certain beetles.

Distribution



A book scorpion (*Chelifer cancroides*) on top of an open book

There are more than 3,300 species of pseudoscorpions recorded in more than 430 genera, with more being discovered on a regular basis. They range worldwide, even in temperate to cold regions like Northern Ontario and above timberline in Wyoming's Rocky Mountains in the United States and the Jenolan Caves of Australia, but have their most dense and diverse populations in the tropics and subtropics. Species have been found under tree bark, in leaf and pine litter, in soil, in tree hollows, under stones, in caves, at the seashore in the intertidal zone, and within fractured rocks.

Chelifer cancroides is the species most commonly found in homes, where they are often observed in rooms with dusty books. There the tiny animals (2.5–4.5 mm or 0.10–0.18 in) can find their food like booklice and house dust mites. They enter homes by "riding along" with larger insects (known as phoresy), or are brought in with firewood.

Evolution

The oldest known fossil pseudoscorpion dates back 380 million years to the Devonian period. It has all of the traits of a modern pseudoscorpion, indicating that the order evolved very early in the history of land animals.

Historical references

Pseudoscorpions were first described by Aristotle, who probably found them among scrolls in a library where they would have been feeding on booklice. Robert Hooke referred to a "Land-Crab" in his 1665 work *Micrographia*. Another reference in the 1780s, when George Adams wrote of: "A lobster-insect, spied by some labouring men who were drinking their porter, and borne away by an ingenious gentleman, who brought it to my lodging."

Classification

This list follows Joel Hallan's Biology Catalog. Number of Recent genera and species are given in parentheses.

- suborder Epiocheirata
 - Chthonioidea
 - Chthoniidae (31, 605)
 - †Dracochelidae – one fossil species (Devonian)
 - Lechytiidae (1, 22)
 - Tridenchthoniidae (17, 68)
 - Fealloidea
 - Feallidae (1, 12)
 - Pseudogarypidae (2, 7)
- suborder Iocheirata
 - infraorder Hemictenata
 - Neobisioidea
 - Bochicidae (10, 38)
 - Gymnobisiidae (4, 11)
 - Hyidae (3, 9)
 - Ideoroncidae (9, 53)
 - Neobisiidae (34, 498)
 - Parahyidae (1, 1)
 - Syarinidae (16, 93)
 - infraorder Panctenata
 - group Ellassommatina

- Cheliferoidea (224, 1261)
 - Atemnidae (19, 172)
 - Cheliferidae (59, 292)
 - Chernetidae (112, 643)
 - Withiidae (34, 154)
- Sternophoroidea
 - Sternophoridae (3, 20)
- group Mestommatina
- Garypoidea
 - Cheiridiidae (6, 69)
 - Garypidae (10, 74)
 - Geogarypidae (3, 61)
 - Larcidae (2, 13)
 - Pseudochiridiidae (2, 12)
- Olpioidea
 - Menthidae (4, 8)
 - Olpiidae (53, 329)
- *incertae sedis*
 - *Megathis* Stecker, 1875 (*nomen dubium*, 2 species)

Chapter 8

Amblypygi

Amblypygi

Temporal range: Upper Carboniferous–Recent



Damon diadema

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Arachnida
Order:	Amblypygi Thorell, 1883

Families

- Paracharontidae
- Charinidae
- Charontidae
- Phrynichidae
- Phrynidae

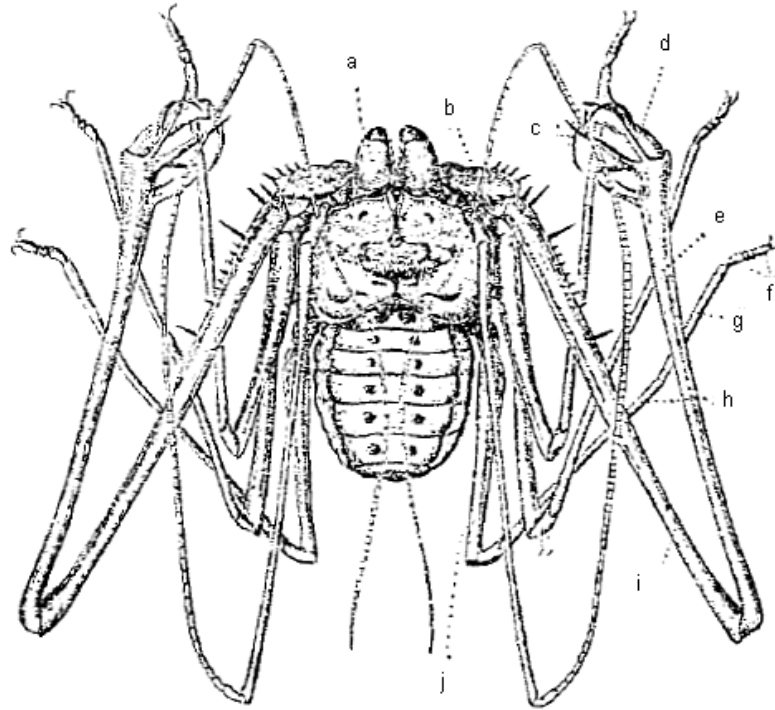
Amblypygi is an order of invertebrate animals belonging to the class Arachnida, in the subphylum Chelicerata of the phylum Arthropoda. They form a separate order of arachnids alongside the spiders, scorpions and others.

Amblypygids are also known as **whip spiders** and **tailless whip scorpions** (not to be confused with whip scorpions that belong to the Arachnid order Thelyphonida). The

name "amblypygid" means "blunt rump", a reference to a lack of the telson ("tail") carried by related species. They are totally harmless to humans.

As of 2003, 5 families, 17 genera and around 155 species have been discovered. 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.

Physical description



Phrynichus phipsoni (male)

a. mandible; l. trochanter; i. femur; e. tibia; d. hand; c. claw of chela; j. femur; h. tibia; g. protarsus; f. tarsus of leg

Parts of an amblypygid, from Pocock (1900)

Amblypygids may range from 4 to 45 millimetres (0.16 to 1.8 in). Their bodies are broad and highly flattened, with a solid carapace and a segmented abdomen. They have a pair of median eyes at the front of the carapace, and three smaller eyes placed further back on each side. The pedipalps are large and somewhat pincer-like, being adapted for grabbing prey.

As in some other arachnid orders, the first pair of legs are modified to act as sensory organs, while the animal uses the other six legs for walking. The sensory legs are very thin, have numerous sensory receptors, and can extend several times the length of body. Typically, the animal holds one of these legs out in front of it as it moves, and uses the

other to probe the terrain to the side. Amblypygids have no silk glands or venomous fangs.

Behaviour

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 masticated with chelicerae.

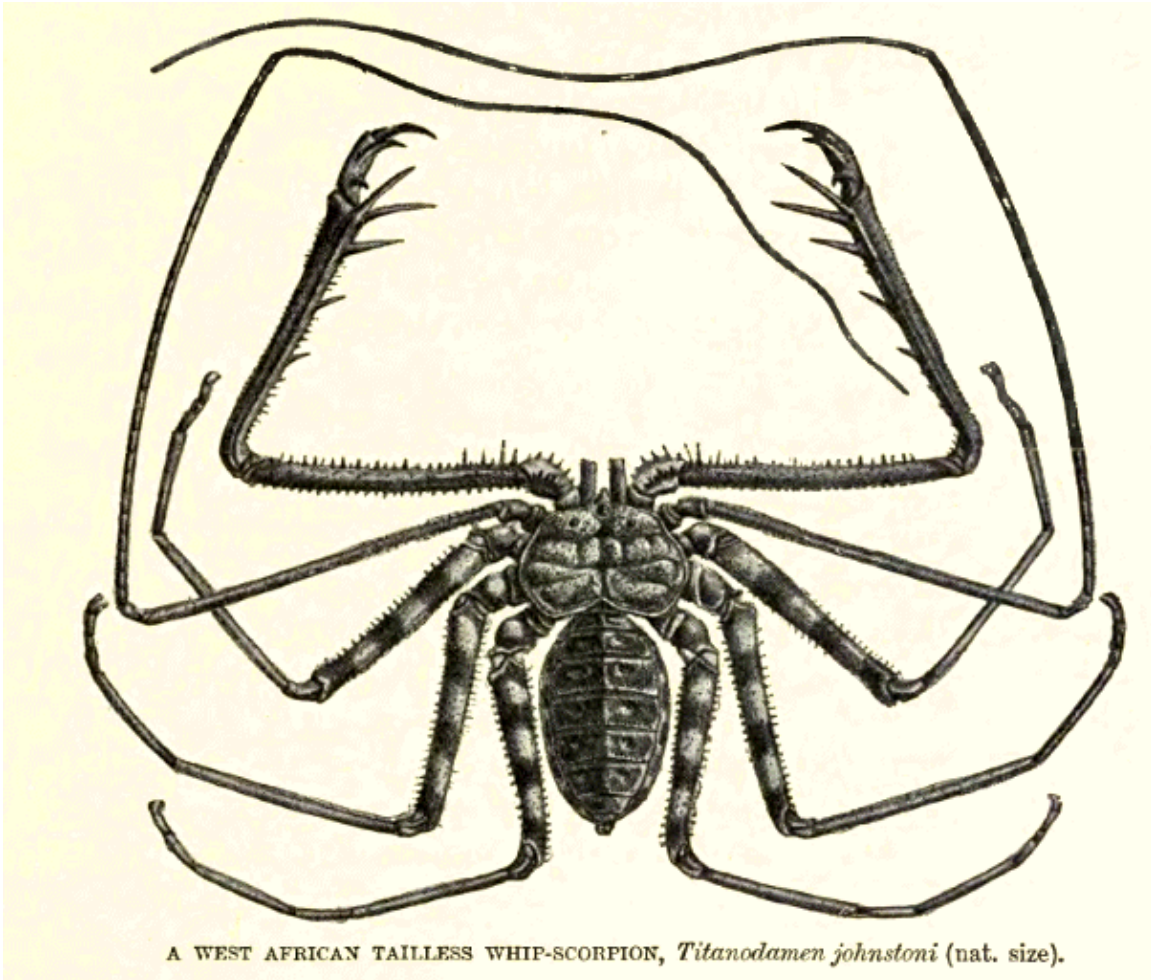
Courting rituals involve the male depositing stalked spermatophores which have one or more sperm masses at the tip on the ground and guiding the female with his pedipalps over them. She gathers the sperm and lays fertilized eggs into a sac carried under the abdomen. When the young hatch, they climb up onto the mother's back; any of which falling off before their first moult will be eaten by the mother.

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 communicate with their young by caressing the offspring with her anteniform front legs. Further, in an experiment where 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.

History

Fossilized amblypygids have been found dating back to the Carboniferous period, for example *Graeophonus*.

Genera



Damon johnstonii from West Africa

The following genera are recognised:

Charinidae Weygoldt, 1996

- *Catageus* Thorell, 1889 (1 species)
- *Charinus* Simon, 1892 (33 species)
- *Sarax* Simon, 1892 (10 species)

Charontidae Simon, 1892

- *Charon* Karsch, 1879 (5 species)
- *Stygophrynus* Kraepelin, 1895 (7 species)

Phrynichidae Simon, 1900

- *Damon* C. L. Koch, 1850 (10 species)
- *Musicodamon* Fage, 1939 (1 species)
- *Phrynichodamon* Weygoldt, 1996 (1 species)
- *Euphrynichus* Weygoldt, 1995 (2 species)
- *Phrynichus* Karsch, 1879 (16 species)
- *Trichodamon* Mello-Leitão, 1935 (2 species)
- *Xerophrynus* Weygoldt, 1996 (1 species)

Phrynidae Blanchard, 1852

- *Heterophrynus* Pocock, 1894 (14 species)
- *Acanthophrynus* Kraepelin, 1899 (1 species)
- †*Electrophrynus* Patrunkevich, 1971 (1 species; Late Oligocene – Early Miocene)
- *Paraphrynus* Moreno, 1940 (18 species)
- *Phrynus* Lamarck, 1801 (28 species, Oligocene - Recent)

Paracharontidae Weygoldt, 1996

- †*Graeophonus* Scudder, 1890 (2-3 species, Carboniferous)
- *Paracharon* Hansen, 1921 (1 species)

incertae sedis

- † *Sorellophrynus* Harvey, 2002 (1 species, Upper Carboniferous)
- † *Thelyphrynus* Petrunkevich, 1913 (1 species, Upper Carboniferous)

Chapter 9

Thelyphonida and Solifugae

Thelyphonida

Vinegarroons



Scientific classification

Kingdom: Animalia

Phylum: Arthropoda

Class: Arachnida

Order: **Thelyphonida**
O. P-Cambridge,
1872

Families

- Gerialinuridae
- Thelyphonidae

Diversity

c. 15 genera, > 100 species

Thelyphonida is an arachnid order comprising invertebrates commonly known as **vinegarroons**. They are often called **uropygids** in the scientific community after the former order Uropygi (which originally also included the order Schizomida). They are also known as **whip scorpions** because of their resemblance to true scorpions and because of their whiplike tails.

Physical description



FEMALE OF BORNEAN WHIP-SCORPION, *Thelyphonus hosei* (nat. size).

Thelyphonus doriae hosei

The name "uropygid" means "tail rump", from Greek ούροπύγιον (*ouropugion*), from ούρα (*oura*) "tail" and πυγή (*puge*) "rump" referring to the whip-like flagellum on the end of the pygidium, a small plate made up of the last three segments of the abdominal exoskeleton.

Vinegarroons range from 25 to 85 mm (0.98 to 3.3 in) in length, with most species not longer than 30 mm (1.2 in); the largest species, of the genus *Mastigoproctus*, reaching 85 mm (3.3 in).

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, a pattern also found in scorpions. Vinegarroons have no venom 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. The acetic acid gives this spray a vinegar-like smell, giving rise to the common name *vinegarroon*.

Vinegarroons are carnivorous, nocturnal hunters feeding mostly on insects and millipedes, but sometimes on worms and slugs. *Mastigoproctus* sometimes preys on small vertebrates. 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 vinegarroons, and leave the burrow; the mother dies soon after. The young grow slowly, going through three molts in about three years before reaching adulthood. They live for up to another four years.

Habitat

Vinegarroons are found in tropical and subtropical and Hot Dry areas worldwide. They are missing in Europe, Australia, and, except for an introduced species, in Africa. They usually dig underground burrows with their pedipalps, to which they transport their prey. They may also burrow under logs, rotting wood, rocks, and other natural debris. They prefer humid, dark places and avoid light.

Subtaxa

As of 2006, over 100 species of vinegarroons have been described worldwide. Subtaxa of vinegarroons currently include only one extant family and a doubtful extinct family:



Mastigoproctus giganteus female with eggs

- Hypoetoninae Pocock, 1899
 - *Etieneus* Heurtault, 1984
 - *Hypoetonus* Thorell, 1888
 - *Labochirus* Pocock, 1894
 - *Thelyphonellus* Pocock, 1894
- Mastigoproctinae Speijer, 1933
 - *Mastigoproctus* Pocock, 1894
 - *Mimoscorpilus* Pocock, 1894
 - *Uroproctus* Pocock, 1894
- Thelyphoninae Lucas, 1835
 - *Abaliella* Strand, 1928
 - *Chajnus* Speijer, 1936
 - *Ginosigma* Speijer, 1936
 - *Glyptogluteus* Rowland, 1973
 - *Minbosius* Speijer, 1933
 - *Tetrabalius* Thorell, 1888
 - *Thelyphonus* Latreille, 1802

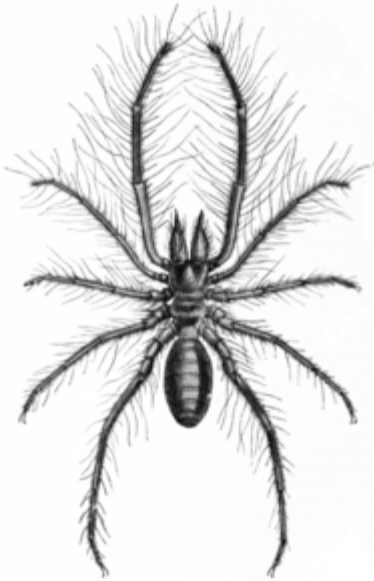
- Typopeltinae Rowland & Cooke, 1973
 - *Typopeltis* Pocock, 1894
- *incertae sedis*
 - † *Geralinura* Scudder, 1884
 - † *Mesoproctus* Dunlop, 1998
 - † *Proschizomus* Dunlop & Horrocks, 1996

Rowland & Cooke (1973) provided a useful synopsis of the order, including a key to genera and a checklist of species. They also presented a novel classification that included the division of the group into two families, Thelyphonidae and Hypoconidae. Weygoldt (1979) suggested the existence of two families was not supported by the available data, and Haupt & Song (1996) formally reduced the Hypoconidae to a subfamily as there was little support for a monophyletic Hypoconidae. Dunlop & Horrocks (1996) suggested that the hypoconids may be the sister-group to the Schizomida and *Proschizomus* Dunlop & Horrocks 1996, but the character polarities they utilized were regarded as uncertain and many features of *Proschizomus* were not observable in the fossilized material.

Solifugae

Solifugae

Temporal range: Late Carboniferous–Recent



A male *Galeodes* (from R. A. Lydekker, 1879)

Scientific classification

Kingdom: Animalia
Phylum: Arthropoda
Class: Arachnida
Subclass: Dromopoda
Order: **Solifugae**
Sundevall, 1833

Solifugae is an order of Arachnida, known as **camel spiders**, **wind scorpions** or **sun spiders**, comprising more than 1,000 described species in about 153 genera. They may grow to a length of 19 cm (7.5 in), and have a body comprising an *opisthosoma* (abdomen) and a *prosoma* (head) with conspicuously large chelicerae, which are also used for stridulation. Most species live in deserts and feed opportunistically on ground-dwelling arthropods and other animals. A number of urban legends exaggerate the size and speed of Solifugae, and their potential danger to humans.

Anatomy



Unidentified solifugid, Arizona

Solifugids are moderate to large arachnids, with the larger species reaching 19 centimetres (7.5 in) in length. The body is divided into a forward part, cephalothorax or prosoma, and a ten-segmented abdomen or opisthosoma. The prosoma comprises the head, mouthparts and somites containing the pedipalps. It is divided into a relatively large anterior carapace, including the animal's eyes, and a smaller posterior section.

The most distinctive feature of Solifugae is their large chelicerae, which are longer than the prosoma. Each of the two chelicerae are composed of two articles forming a powerful pincer; each article bears a variable number of teeth.

While solifuges appear to have ten legs, they have eight legs like other arachnids; the first set of appendages are pedipalps, which function as sense organs similar to insects' antennae and give the appearance of an extra pair of legs. The pedipalps terminate in eversible adhesive organs, which are used to capture flying prey, and for climbing. They stridulate with their chelicerae, resulting in a rattling noise.

Of the four pairs of legs, the first pair are smaller in size, and act as accessory tactile organs used to feel the animal's surroundings, so that only the other six legs are used for running. On the last pair of legs, Solifugae have fan-shaped sensory organs called as *racquet organs* or malleoli.

Like pseudoscorpions and harvestmen, they lack book lungs, having instead a well-developed tracheal system that takes in air through three pairs of slits on the animal's underside. In some species there are very large central eyes that are capable of recognising forms, and are used for hunting. Lateral eyes are only rudimentary, if present at all. Males are usually smaller than females, with longer legs.

Classification

Solifugae are not true spiders, which are from a different order, Araneae. Like scorpions and harvestmen, they belong to a distinct arachnid order. There are about 1065 species of solifuges known, grouped in about 153 genera and 12 families belonging to the order Solifugae:

- Ammotrechidae
- Ceromidae
- Daesiidae
- Eremobatidae
- Galeodidae
- Gylippidae
- Hexisopodidae
- Karschiidae
- Melanoblossidae
- Mummuciidae
- Rhagodidae
- Solpugidae

The family Protosolpugidae is only known from one fossil species from the Pennsylvanian.

Ecology



Gluvia dorsalis eating a cabbage bug (*Eurydema oleraceum*)

Although Solifugae are considered to be endemic indicators of desert biomes, some species have been known to live in grassland or forest habitats. Most solifugae inhabit warm and arid habitats, including virtually all deserts in both the Eastern and Western Hemispheres, but excluding Australia.

Solifugae are carnivorous or omnivorous, with most species feeding on termites, darkling beetles, and other small ground-dwelling arthropods. Solifuges are opportunistic feeders and have been recorded as feeding on snakes, small lizards and rodents; Solifugae have even been videotaped consuming 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. Although they do not normally attack humans, these chelicerae can penetrate human skin, and painful bites have been reported.

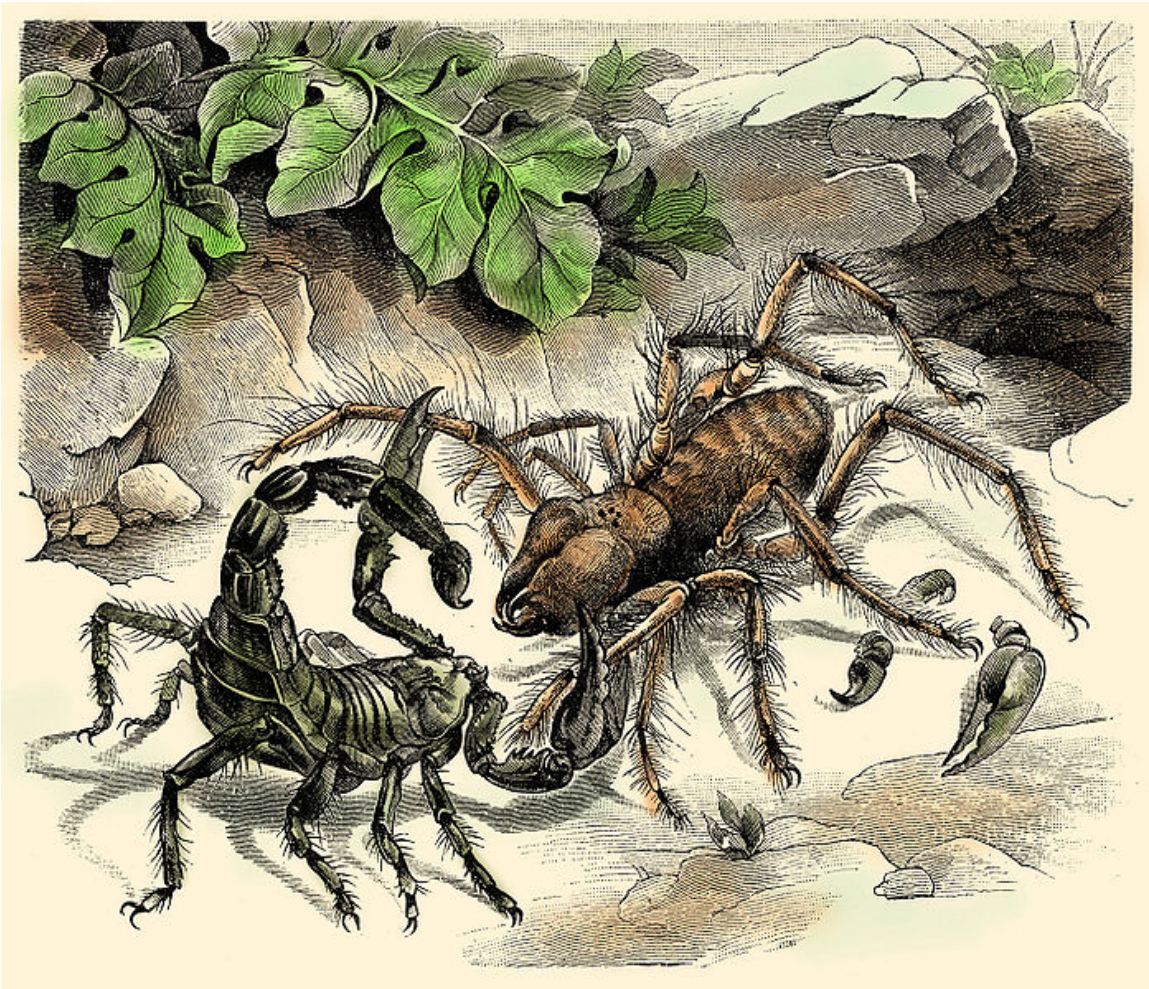
Life cycle

Solifugae are typically univoltine. 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. To do this, he flings the female on her back. The female then digs a burrow, into which she lays 50 to 200 eggs. Depending on the species, she guards them until they hatch. Because the female will not feed during this time, she will try to fatten herself beforehand, and a species of 5 centimetres (2.0 in) has been observed to eat more than 100 flies during that time in the laboratory. Solifugae undergo a number of stages including, egg, post-embryo, nine to ten nymphal instars, and adults.

Etymology

The name *Solifugae* derives from Latin, and means "those that flee from the sun". The order is also known by the names Solpugida, Solpugides, Solpugae, Galeodea and Mycetophorae. Their common names include *camel spider*, *wind scorpion*, *jerry muglum*, *sun scorpion* and *sun spider*. In southern Africa they are known by a host of names including *red romans*, *haarskeerders* and *baardskeerders*, the latter two relating to the belief they use their formidable jaws to clip hair from humans and animals to line their subterranean nests.

Solifugids and humans



A scorpion (left) fighting a solifugid (right)

Solifugids have been recognised as distinct taxa from ancient times. The Greeks recognised that they were distinct from spiders; spiders were called ἀράχνη (*arachne*) while Solifugae were named φαλάγγιον (*phalangion*). In Aelian's *De natura animalium* they are mistakenly mentioned, along with scorpions, as responsible for the abandoning of a country in Ethiopia. Anton August Heinrich Lichtenstein theorised in 1797 that the "mice" which plagued the Philistines in the Old Testament were Solifugae. During World War I, troops stationed in Abū Qīr, Egypt would stage fights between captive *jerrylanders*, as they referred to them and placed bets on the outcome. Similarly British troops stationed in Libya in World War II would stage fights between Solifugae and scorpions.

Urban legends



An unidentified solifugid against a ruler, marked in inches

Solifugae are the subject of many urban legends and exaggerations about their size, speed, behaviour, appetite, and lethality. They are not especially large, the biggest having a leg span of perhaps 12 centimetres (4.7 in). They are fast on land compared to other invertebrates. The fastest can run perhaps 16 km/h (10 mph) for a short distance, nearly half as fast as the fastest human sprinter. Members of this order of Arachnida apparently have no venom, with the possible exception of one species in India (*Rhagodes nigrocinctus*) as suggested in one study and do not spin webs.

In the Middle East, it is widely rumored among American and coalition military forces stationed there that Solifugae will feed on living human flesh. The story goes that the creature will inject some anaesthetising venom into the exposed skin of its sleeping victim, then feed voraciously, leaving the victim to awaken with a gaping wound. Solifugae, however, do not produce such an anaesthetic, and they do not attack prey larger than themselves unless threatened. Other stories include tales of them leaping into the air, disemboweling camels, screaming, and running alongside moving humvees; all of these tales are false.

Due to their bizarre appearance many people are startled or even afraid of them. This fear was sufficient to drive a family from their home when one was discovered in a soldier's

house in Colchester, England and caused the family to blame the death of their pet dog on the solifugid. The greatest threat they pose to humans, however, is their bite in self-defense when one tries to handle them. There is essentially no chance of death directly caused by the bite, but, due to the strong muscles of their chelicerae, they can produce a proportionately large, ragged wound that is prone to infection.

Chapter 10

Xiphosura



Horseshoe crab (*Limulus polyphemus*)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Merostomata
Order:	Xiphosura Latreille, 1802

Xiphosura is an order of marine chelicerates which includes a large number of extinct lineages and only four recent species in the family Limulidae, which include the horseshoe crabs. The group has hardly changed in millions of years; the modern horseshoe crabs look almost identical to prehistoric genera such as the Jurassic *Mesolimulus*, and are considered to be living fossils.

Xiphosura are traditionally placed in the class Merostomata, although this term was originally intended to encompass also the eurypterids, whence it denoted what is now known to be an unnatural (paraphyletic) group. Although the name Merostomata is still

seen in textbooks, without reference to the Eurypterida, some have urged that this usage should be discouraged.

Description

Modern xiphosurans reach up to 60 centimetres (24 in) in adult length, but the Paleozoic species were often far smaller, some as little as 1 to 3 centimetres (0.39 to 1.2 in) long.

The body is covered with heavy mineralized cuticle, and is divided into an anterior prosoma and a posterior opisthosoma, or abdomen. The upper surface of the prosoma is covered by a semicircular carapace, while the underside bears five pairs of walking legs and a pair of pincer-like chelicerae. The mouth is located below the forward tip of the carapace, and lies behind a lip-like structure called the labrum.

Xiphosurans have up to four eyes, located in the carapace. There are a pair of compound eyes on the side of the prosoma, and one or two median ocelli towards the front. The compound eyes are simpler in structure than those of other arthropods, with the individual ommatidia not being arranged in a compact pattern. They can probably detect movement, but are unlikely to be able to form a true image. In front of the ocelli is an additional organ that probably functions as a chemoreceptor.

The first four pairs of legs end in pincers, and have a series of spines, called the gnathobase, on the inner surface. The spines are used to masticate the food, tearing it up before passing it to the mouth. The fifth and final pair of legs, however, have no pincers or spines, instead having structures for cleaning the gills and pushing mud out of the way while burrowing. Behind the walking legs are a sixth set of appendages, the *chilaria*, which are greatly reduced in size and covered in hairs and spines. These are thought to be vestiges of the limbs of an absorbed first opisthosomal segment.

The opisthosoma is divided into a forward mesosoma, with flattened appendages, and a metasoma at the rear, which has no appendages. In modern forms, the whole of the opisthosoma is fused into a single unsegmented structure. The underside of the opisthosoma carries the genital openings and five pairs of flap-like gills.

The opisthosoma terminates in a long caudal spine, commonly referred to as a telson (though this same term is also used for a different structure in crustaceans). The spine is highly mobile, and is used to push the animal upright if it is accidentally turned over.

Internal anatomy

The mouth opens into a sclerotised oesophagus which leads to a crop and gizzard. After grinding up its food in the gizzard, the animal regurgitates any inedible portions, and passes the remainder to the true stomach. The stomach secretes digestive enzymes, and is attached to an intestine and two large caeca that extend through much of the body, and absorb the nutrients from the food. The intestine terminates in a sclerotised rectum, which opens just in front of the base of the caudal spine.

Xiphosurans have a well developed circulatory system, with numerous arteries that send blood from the long tubular heart to the body tissues, and then to two longitudinal sinuses next to the gills. After being oxygenated, the blood flows into the body cavity, and back to the heart. The blood contains haemocyanin, a blue copper-based pigment performing the same function as haemoglobin in vertebrates, and also has blood cells that aid in clotting.

The excretory system consists of two pairs of coxal glands connected to a bladder that opens near the base of the last pair of walking legs. The brain is relatively large, and, as in many arthropods, surrounds the oesophagus. In both sexes, the single gonad lies next to the intestine and opens on the underside of the opisthosoma.

Reproduction

Xiphosurans move to shallow water to mate. The male climbs onto the back of the female, gripping her with his first pair of walking legs. The female digs out a depression in the sand, and lays from 200 to 300 eggs, which the male covers with sperm. The pair then separate, and the female buries the eggs.

The eggs are about 2–3 millimetres (0.08–0.12 in) across, and hatch into a larva that superficially resembles a trilobite. Indeed it is often referred to as the 'trilobite larva'. Through a series of successive moults, the larva develops additional gills, increases the length of its caudal spine, and gradually assumes the adult form. Modern xiphosurans reach sexual maturity after about three years of growth.

Classification of the Xiphosura

Order Xiphosura Latreille, 1802

- †Suborder Synziphosurida
 - Weinberginidae Richter & Richter, 1929 (Lower Devonian)
 - Bunodidae Packard, 1886
 - Bunodinae Packard, 1886 (Upper Silurian to Downtonian)
 - Limuloidinae Størmer, 1952 (Upper Silurian)
 - Pseudoniscidae Packard 1886 (Upper Silurian)
 - Kasibelinuridae Pickett, 1993 (Middle Devonian to Late Devonian)
- Suborder Xiphosurida
 - †Infraorder Bellinurina
 - Elleriidae Raymond, 1944 (Upper Devonian to Upper Carboniferous)
 - Euproopidae Eller, 1938 (= Liomesaspidae Raymond 1944) (Upper Carboniferous to Lower Permian)
 - Bellinuridae Zittel & Eastman, 1913 (Middle Devonian to Upper Carboniferous)
 - Infraorder Limulina
 - †Rolfeiidae Selden & Siveter, 1987 (Early Carboniferous to Early Permian)

- †Paleolimulidae Raymond, 1944 (Carboniferous to Permian)
- †Moravuridae Pribyl, 1967 (Mississippian)
- †Austrolimulidae + †Heterolimulidae (Middle Triassic)
- Limulidae Zittel, 1885
 - †Mesolimulinae Størmer, 1952 (Lower Triassic to Cretaceous)
 - Limulinae Zittel, 1885
 - Tachypleini Pocock, 1902 (Miocene to **Recent**)
 - Limulini Zittel, 1885 (**Recent**)

Taxa removed from Xiphosura

There are two groups originally included in the Xiphosura, but which have been assigned to separate classes:

- Aglaspida Walcott, 1911 (Cambrian to Ordovician)
- Chasmataspida Caster & Brooks, 1956 (Lower Ordovician)

Chapter 11

Sea Spider

Sea spiders

Temporal range: Late Cambrian–Recent



Scientific classification

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

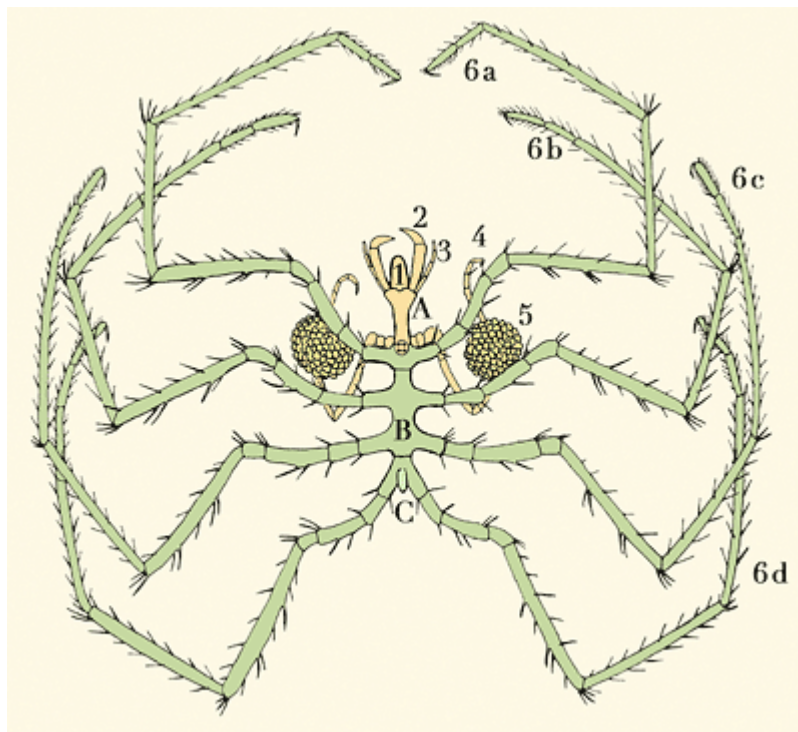
Families

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

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

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

Description



Anatomy of a pycnogonid:

A: head; **B:** thorax; **C:** abdomen

1: proboscis; **2:** chelifores; **3:** palps; **4:** ovigers; **5:** egg sacs; **6a–6d:** four pairs of legs

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

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

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

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

Reproduction and development

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

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

At least four types of larvae have been described: the typical protonymphon larva, the encysted larva, the atypical protonymphon larva, and the attaching larva. The typical protonymphon larva is most common, is free living and gradually turns into an adult. The encysted larva is a parasite that hatches from the egg and finds a host in the shape of a

polyp colony where it burrows into and turns into a cyst, and will not leave the host before it has turned into a young juvenile.

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

Distribution and ecology



A pycnogonid in its natural habitat

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

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

Classification

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

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

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

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

Fossil record

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

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

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