Chelicerata (Arachnids, Including Spiders, Mites and Scorpions)

Introductory article

Article Contents

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Chelicerata is the group of arthropods that includes the marine sea-spiders and horseshoe crabs and the terrestrial arachnids (spiders, mites, scorpions and their relatives). They have two main body regions, and the arachnids typically have eight walking legs. They are covered by a jointed exoskeleton and grow by periodic moulting. Chelicerates are typically predaceous and most terrestrial forms ingest only liquefied food. Next to insects, they are the most diverse and numerous animals.

Basic Design

External anatomy

The chelicerate body is entirely covered with an exoskeleton of cuticle formed primarily from chitin and proteins. It is divided into two basic regions, the prosoma and opisthosoma (**Figure 1**). The prosoma is typically composed of six appendage-bearing segments and an unknown number of anterior segments without appendages. The prosoma is typically covered dorsally by a large plate (carapace), while the ventral surface is formed by the bases of the appendages and ventral plates (sternites). The first pair of prosomal appendages is the chelicerae, which serve as the primary feeding organs. In their primitive form, the chelicerae are composed of three segments, with the terminal two forming a chela or pincer, but the chelicerae of many modern groups (e.g. spiders) have only two segments. The other appendages are multisegmented and typically function as legs, but some are specialized as antenna-like structures or are used in capturing prey.

The opisthosoma is thought to be formed originally from at least 12 segments and a terminal telson and is typically covered dorsally by a segmental series of plates (tergites) and ventrally by another series of plates (sternites). External indication of the original segmentation is reduced or lost in most spiders, mites and certain other groups. The genital opening generally occurs on the ventral surface of the second opisthosomal segment and is sometimes associated with appendages. Appendages may have been present on the ventral surface of most opisthosomal segments in primitive chelicerates, but well-developed opisthosomal appendages are retained in only a few living groups (e.g. gill plates in horseshoe crabs and silk-producing spinnerets in spiders).

Internal anatomy and physiology

The skeleton of chelicerates consists of internal projections from the cuticle and a horizontal sheet of tendinous connective tissue, the endosternite (**Figure 2**). Both serve as sites for muscle attachment. The body fluid (haemolymph) can also act as a hydrostatic skeleton. Contraction of certain muscles associated with the endosternite raises internal pressure, and the animal can use this pressure to move parts of the body. For example, spiders do not have extensor muscles in their spinnerets and certain leg joints and use fluid pressure in moving these appendages.

The digestive tract varies considerably in different chelicerate groups. There is generally some kind of preoral chamber in which food is macerated and liquefied by secreted salivary enzymes. The mouth opens into this preoral chamber beneath a cuticular lobe (labrum) and enters a cuticle-lined pharynx operated by constrictor and dilator muscles. The pharynx acts as a crop and gizzard in the aquatic horseshoe crabs but serves as a suctorial fluid pump in most terrestrial chelicerates. The pharynx then empties into a midgut that lacks cuticular lining. The midgut typically has one or more diverticula or caeca and these appear to be the principal sites of digestion and nutrient absorption. The midgut opens to a cuticle-lined hindgut where fluid and ion balance are regulated. The anus opens on the last opisthosomal segment.

There are two main types of excretory organs, namely coxal glands and Malpighian tubules. Coxal glands are involved primarily in ion regulation and water balance. They occur in many different chelicerates and appear to be homologous with the nephridia of other invertebrates. Fluid from coxal glands exits through small pores located on or near the basal segments (coxae) of the legs. The fluid is sometimes used as saliva. Malpighian tubules are present

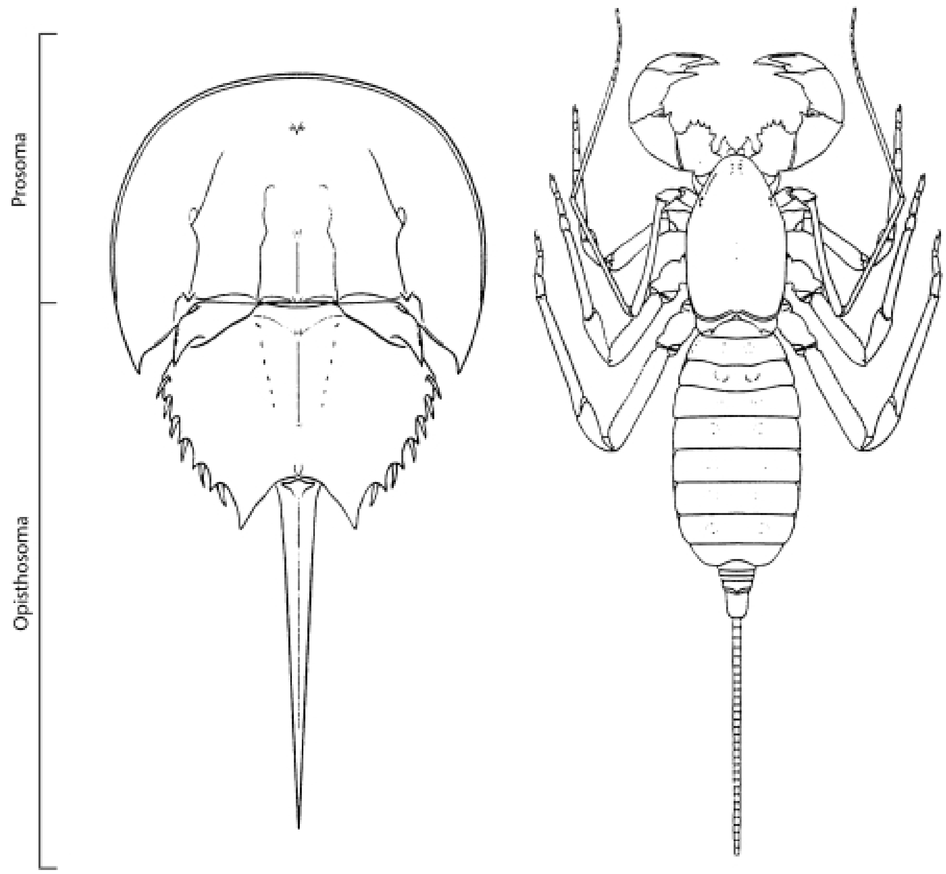

Figure 1 Two living chelicerates, the Atlantic horseshoe crab (*Limulus polyphemus*: Xiphosura) and the giant whipscorpion (*Mastigoproctus giganteus*: Arachnida, Thelyphonida). Dorsal perspectives.

in many terrestrial chelicerates. These tubes are thought to be derived from midgut diverticula, and they produce a fluid that contains nitrogenous waste which is concentrated in the hindgut.

The respiratory system of ancestral chelicerates probably consisted of gills arranged on the opisthosomal appendages. These gills are retained in horseshoe crabs, where they are called book gills due to the similarity of the gill lamellae to the pages of a book. Similar structures have been internalized in some terrestrial groups (e.g. spiders and scorpions) and are called book lungs. Many terrestrial chelicerates respire through thin-walled cuticular tubes (tracheae) that open to the air through pores (stigmata or spiracles). Tracheal systems appear to have evolved several times in terrestrial chelicerates. Sea-spiders and some very small terrestrial chelicerates do not have specialized respiratory organs.

Like all arthropods, chelicerates have an ‘open’ circulatory system, in which the haemolymph is not contained within a closed system of arteries and veins but flows at some point into the general body cavity (haemocoel). The vascular system generally consists of a dorsal tubular heart that pumps haemolymph from the opisthosoma to the prosoma. Haemolymph from the heart is sometimes distributed throughout the body by an extensive arterial network, especially in those chelicerates with book gills or book lungs. The haemolymph is then directed through a network of cavities and sinuses that lead to the gills or lungs and back to the heart. The circulatory system is generally much simpler in smaller chelicerates and in those that respire through tracheae.

The central nervous system is ventral and consists of a series of paired ganglia (one pair per body segment)

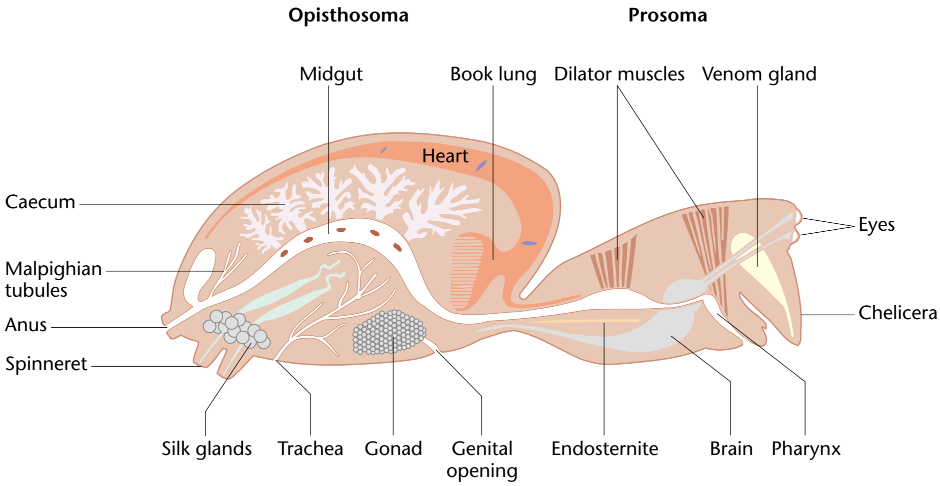

Figure 2 A diagrammatic sagittal section of a spider showing the major internal organs.

connected longitudinally by paired nerve cords. The ganglia in many groups tend to migrate anteriorly into the prosoma to form a single neural mass ('brain'). The visual system in primitive chelicerates consists of two medial eyes with a single lens and two lateral eyes with multiple lenses, but one or both kinds of eyes are usually simplified or lost in terrestrial groups. Chelicerates have many kinds of sense organs that detect mechanical forces (mechanoreceptors). Terrestrial chelicerates have unique mechanoreceptors called slit sensilla, which appear as small slits in the cuticle. The sensory cells associated with these sensilla respond to compressional forces acting perpendicular to the long axis of the slit. Many slits may be aligned near a joint to form a lyriform organ. Terrestrial chelicerates also have a wide variety of sensilla derived from hair-like structures (setae). Trichobothria are long setae that are jointed at the base and are easily displaced by air movements, such as those created by potential prey or predators.

Diversity

Chelicerata is divided into four major groups or classes, namely Pycnogonida or Pantopoda (sea-spiders), Xiphosura (horseshoe crabs and extinct relatives), Eurypterida (extinct sea-scorpions) and Arachnida (mainly terrestrial chelicerates including spiders, scorpions, mites, etc.). Except for insects, chelicerates are probably the most taxonomically diverse group of animals. Among the living marine chelicerates, there are about 500 known species of pycnogonids and four species of xiphosurans. The arachnids are divided into 11 orders. There are approximately 32 000 described species in Acari (mites), 100 in Amblypygi (whipspiders), 34 000 in Araneae (spiders), 5000 in Opiliones (harvestmen), 60 in Palpigradi (microwhipscorpions), 3200 in Pseudoscorpiones (false scorpions), 60 in Ricinulei, 180 in Schizomida (small whipscorpions), 1400 in Scorpiones (true scorpions), 900 in Solifugae (sun- or camel-spiders), and 90 in Thelyphonida (large whipscorpions and vinegaroons).

Habitats and Abundance

Pycnogonids (sea-spiders) occur in a wide variety of marine environments from polar to tropical regions and from the intertidal zone to the deep sea. They typically occur on the sea floor or on surfaces of submerged objects. Their abundance varies with habitat. Pycnogonids are probably important members of deep-sea and polar ecosystems.

Xiphosurans occur in marine near-shore environments on the eastern coasts of North America and Asia. Xiphosurans can be very abundant. Atlantic horseshoe crabs (*Limulus*) were once harvested as a source of fertilizer, and their eggs are an important food source for migrating birds. Horseshoe crab populations in both North America and Asia have decreased owing to pollution and coastal development.

The arachnids are one of the largest and most diverse groups of arthropods and occupy all manner of terrestrial environments. A few forms occur in aquatic or intertidal environments. Arachnids, especially spiders and mites, are very abundant in many terrestrial ecosystems and can have a substantial impact on populations of other terrestrial organisms.

Habits and Life Histories

Pycnogonids feed on small organisms that grow on submerged surfaces using their chelicerae (chelifores) and a long proboscis. Life histories are known for relatively few species. Near-shore species tend to have specific annual mating periods, but those off-shore may reproduce year round. Sexes are separate and fertilization is external. Unlike most chelicerates, both eggs and sperm are released from openings at the bases of the legs. The males of many groups carry the eggs in a large mass with specialized appendages (ovigers), and paternal care often continues after the eggs have hatched and the simple protonymphon larva has emerged. The larva undergoes metamorphosis and several moults in which body segments and legs are added. Most species complete development with four pairs of legs but some have five or six pairs.

Xiphosurans live on the sea floor and feed on worms and molluscs. Adults migrate to the shoreline to mate. Males (one or more) grasp the opisthosoma and telson of a female with their specialized first legs and follow the female onto the beach. The female lays eggs in the sand and the males deposit sperm over them. The developing young pass through several molts within the egg before emerging as 'trilobite' larvae, whereupon they return to the ocean. They moult several times before and after reaching maturity. Sexual maturation occurs in 9–12 years, and an individual may live for nearly 20 years.

Arachnids are extremely diverse in both lifestyle and life history. Most are predators, liquefying their prey before consumption, but some (especially mites) are herbivorous or parasitic. The sexes are separate and fertilization is internal. However, methods of sperm transfer vary considerably. Males may produce sperm droplets or a sperm package that are placed on the substrate (e.g. scorpions, pseudoscorpions, whipscorpions and many mites). Others transfer sperm directly via specialized appendages or gonopods (e.g. spiders and ricinuleids) or may copulate directly with the female using a penis (e.g. harvestmen). Sperm transfer is often preceded by courtship displays. Scorpions and some pseudoscorpions have an elaborate 'mating dance' in which the male grasps the claws of the female with his own and manoeuvres the female over his sperm package. Eggs may be left unattended, encased or retained in the body. Viviparity is present in most scorpions. The life cycle may vary in duration from a few weeks to many years, as in the case of some large spiders, scorpions and whipscorpions.

Methods for capturing prey are also very diverse. Many arachnids have appendages specialized for seizing and restraining prey, and some have venoms to immobilize struggling animals. Spiders inject venom through the cheliceral fangs, scorpions use their specialized telson or stinger, and most pseudoscorpions have venom glands in their large chelate claws. These venoms are usually harmless to humans but a few are deadly. Spiders also use a variety of silken structures to detect and entangle prey. Most tarantula-like spiders live in silk-lined burrows and rush out to capture passing insects, but very few construct webs. The webs of other spiders occur in a wide variety of forms, with the orb web being specialized for capturing flying insects.

Of all the arachnids, the mites are the most numerous and probably have the greatest impact on human activities. Some mites are important plant pests that damage agricultural or ornamental plants either directly by their feeding or through transmission of disease. Some mites, especially ticks, can carry human disease. Dust mites are common in human habitations, where they feed on the sloughed skin of people and other organic material. Their faeces are an important cause of allergies in humans. Some microscopic mites even inhabit facial pores and hair follicles of people. However, the vast majority of mites are harmless or beneficial. In fact, certain predaceous mites are cultured specifically for use in controlling arthropod pests, including other mites.

Fossil History

One of the earliest chelicerate-like arthropod fossils (*Sanctacaris uncata*) was discovered in Cambrian-age rocks deposited about 540 million years ago (Ma). The segmental composition of the apparent prosoma and opisthosoma is similar to that of chelicerates, but few other chelicerate features (e.g. chelicerae) are preserved in the known fossils. Several other chelicerate or chelicerate-like fossils are also known from the Early Palaeozoic, but their true phylogenetic affinities are unclear. A fossil group called the Aglaspidida was once placed in Chelicerata but has been shown not to have the requisite characteristics.

The earliest fossil pycnogonids have been found in rocks deposited in the Early Devonian (~ 395 Ma). They have long legs and a reduced opisthosoma like living sea-spiders, but, in contrast to modern forms, the opisthosoma retains external evidence of segmentation.

The fossil history of xiphosurans extends to the Early Ordovician (~ 525 Ma), and fragmentary remains suggest that the group occurred even earlier. Early fossil members of the group had a basic design characteristic of chelicerates in general, but they show a trend towards the incorporation of the anterior opisthosomal segments into the prosoma and the reduction and consolidation of the remaining opisthosomal segments. Modern xiphosurans show the culmination of this trend (**Figure 1**).

The Eurypterida (sea-scorpions) are an extinct group that ranged from the Early Ordovician to the end of the Permian (490–245 Ma). Some members of this group resemble true scorpions in having an opisthosoma divided into a wide anterior region (mesosoma) and narrow posterior region (metasoma), but this similarity is not thought to indicate a close relationship. The last pair of legs is modified into paddles in many species.

The earliest known fossil arachnids (scorpions) were recovered from Silurian rocks deposited about 440 Ma.

These scorpions differ from modern forms in having compound eyes and in being aquatic rather than terrestrial. The oldest fossil spiders, pseudoscorpions and mites are from the Early Devonian ($\sim$390 Ma), and the oldest fossil whipspiders, harvestmen, ricinuleids, camel-spiders and whipscorpions are from the Middle Carboniferous (300–325 Ma). Fossil Palpigradi and Schizomida have only been found in relatively recent deposits. There are several spider-or mite-like arachnid groups known only from fossils, including Haptopoda, Phalangiotarbida and Trigonotarbida. The oldest clearly terrestrial arachnid is a trigonotarbid from the Late Silurian ($\sim$410 Ma).

Phylogeny

The living chelicerates form a clearly defined group that may be closely related to trilobites. Some workers have doubted whether pycnogonids are true chelicerates, but recent molecular analyses have shown that they are more closely related to chelicerates than to any other arthropod group. Pycnogonids appear to be the sister group to all other living chelicerates.

Living xiphosurans also form a well-defined group, but most of its members are extinct. Placement of some fossil xiphosurans is problematic because many characteristics used in classification are not preserved in the known fossils. Among living xiphosurans, the three Asian species are more closely related to each other than to the single Atlantic species. Xiphosurans appear to be the sister group to Eurypterida and Arachnida.

Eurypterida was once placed with xiphosurans in a group called Merostomata, but this classification has been abandoned. Most workers now consider Eurypterida to be more closely related to arachnids than to xiphosurans. However, there is debate as to whether Eurypterida is most closely related to all arachnids or to scorpions only.

The phylogeny of arachnids is controversial, but several well-defined relationships have been established. Whipspiders (Amblypygi) and whipscorpions (Schizomida and Thelyphonida) appear to form a group that is most closely related to spiders. The extinct trigonotarbids are closely related to spiders, whipspiders and whipscorpions. Pseudoscorpiones and Solifugae are sister groups. Recent morphological and molecular systematic analyses suggest the Opiliones and Scorpiones are closely related to each other and to the Pseudoscorpiones–Solifugae group. However, as noted above, placement of Scorpiones in chelicerate phylogeny is unsettled.

Further Reading

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