= Chelicerata =

The subphylum Chelicerata (/ k??l?s??re?t? / or / k??l?s??r??t? / ; New Latin , from French chélicère , from Greek kh?l? " claw , chela " and kéras " horn ") constitutes one of the major subdivisions of the phylum Arthropoda . It contains the horseshoe crabs , sea spiders , and arachnids (including scorpions and spiders) .

The chelicerata 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 pycnogonids (sea spiders) , if the latter are indeed 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 prosoma and the opisthosoma , 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 to feed . However , spiders ' chelicerae form fangs that most species use to inject venom into prey . The group has the open circulatory system typical of 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 that 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 . 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 prosoma or cephalothorax , and the rear tagma is called the opisthosoma or abdomen . However , in the Acari (mites and ticks) there is no visible division between these sections .

The prosoma 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 opisthosoma consists of twelve or fewer segments that originally formed two groups , a mesosoma of seven segments and a 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 chemically hardened proteins . Since this cannot stretch , the animals must molt to grow . In other words , they grow new but still soft cuticles , then cast off the old one and wait for the new one to harden . Until the new cuticle hardens the animals are defenseless and almost immobilized .

= = = 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 fossil eurypterids and modern harvestmen form 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 they excrete as dry matter . Extraction is 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 = = =

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 . If one assume that chelicerates lose the first segment , which bears antennae in other arthropods , chelicerate brains include only one pair of pre @-@ oral ganglia instead of two . However , there are evidences that the first segments is available indeed and bears the cheliceres .
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 prosoma plus those of the first two opisthosomal segments , while the other opisthosomal segments retain separate pairs of ganglia . In most living arachnids , except scorpions if they are true arachnids , all the ganglia , including those that would normally be in the opisthosoma , are fused into a single mass in the prosoma and there are no ganglia in the opisthosoma . However , in the Mesothelae , which are regarded as the most primitive living spiders , the ganglia of the opisthosoma and the rear part of the prosoma 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 (only in horseshoe crabs , as the compound eye in the other clades has been reduced to a cluster of no more than five pairs of ocelli) , mounted on the sides of the head , plus 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 and is able to see in both colors and UV @-@ light .

= = = Reproduction = = =

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 .

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 . Rather , it was likely sister group to the spiders , a clade which has been named Serikodiastida . 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 . Cladistic analyses have recovered Proscorpius within the scorpions , based on reinterpretation of the species ' breathing apparatus . This is reflected also in the reinterpretation of Palaeoscorpius as a terrestrial animal .

= = 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 .

= = Interaction with humans = =

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 . Horseshoe crab blood contains a clotting agent , limulus amebocyte lysate , which is used to test antibiotics and kidney machines to ensure they 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 .