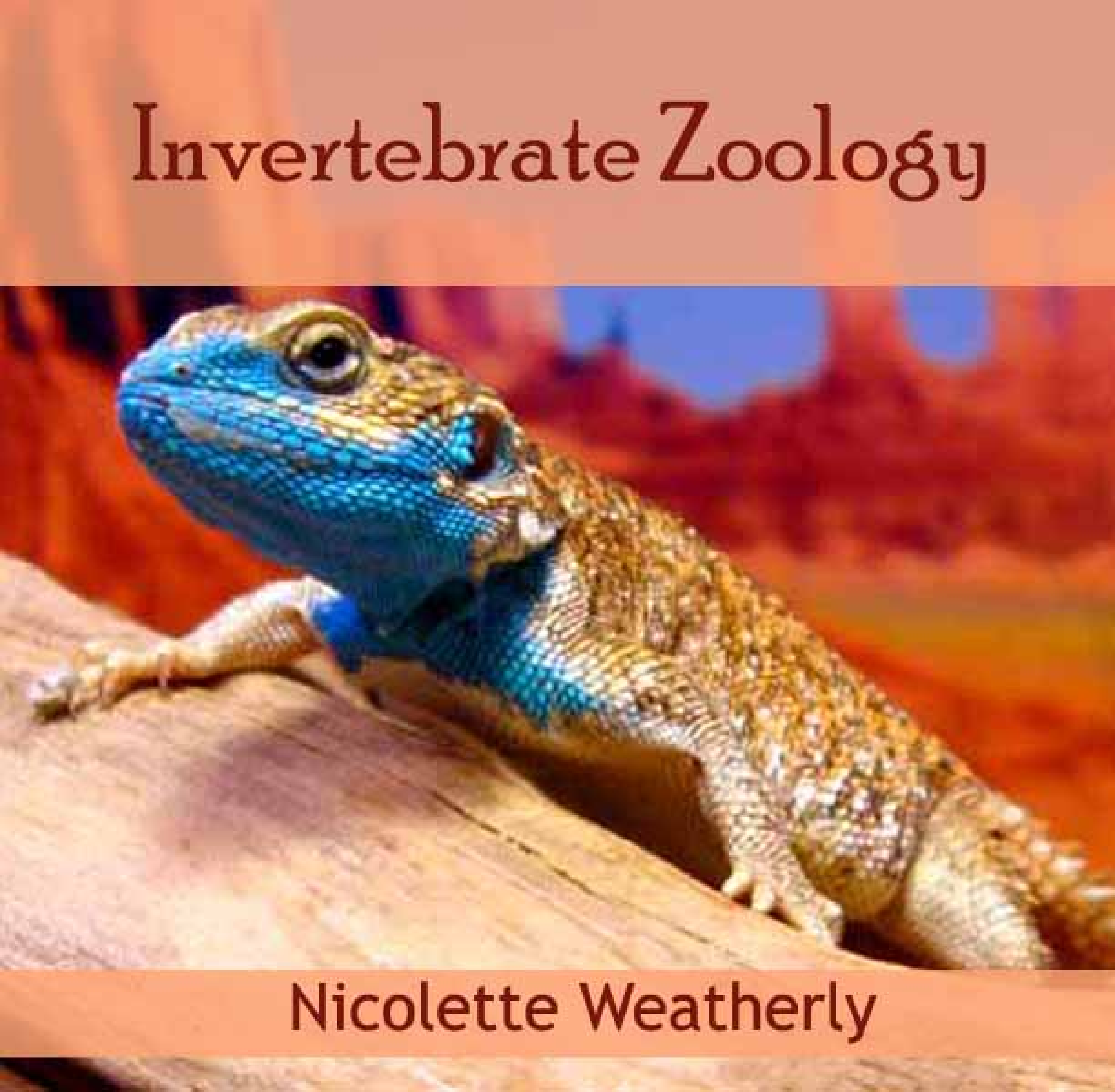
Invertebrate Zoology



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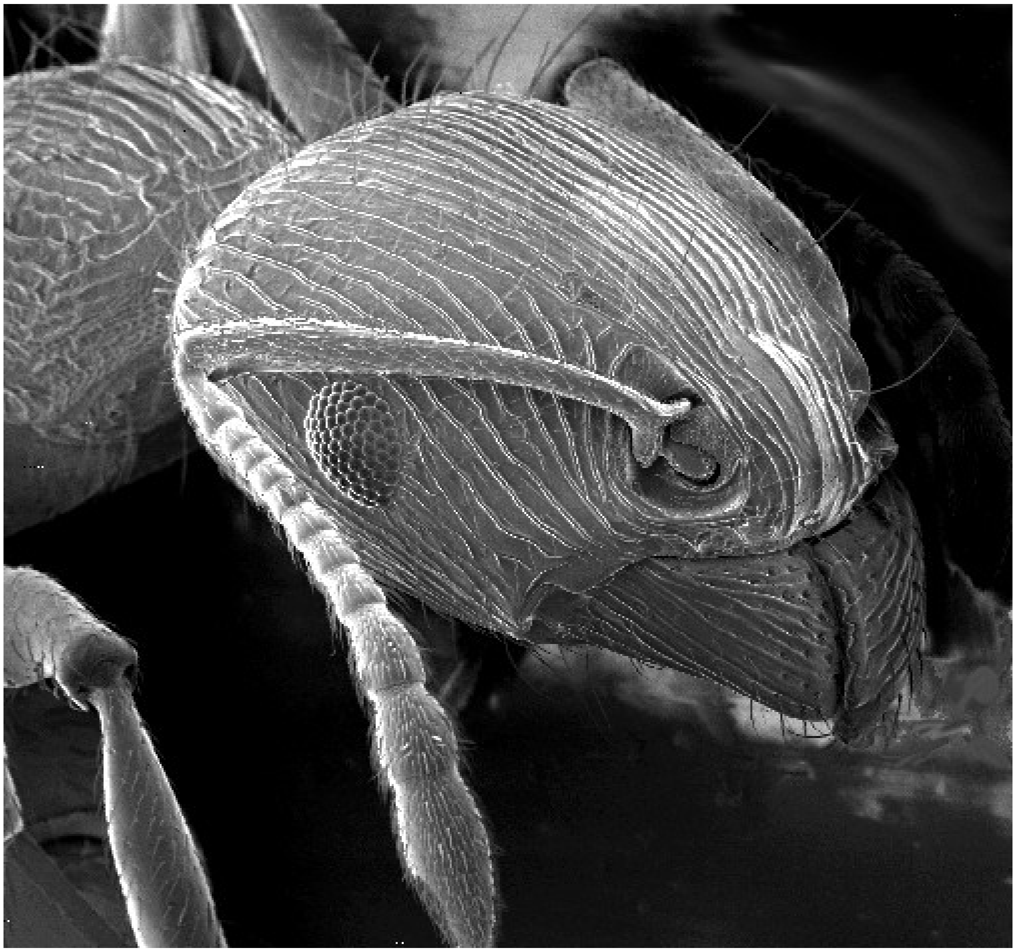
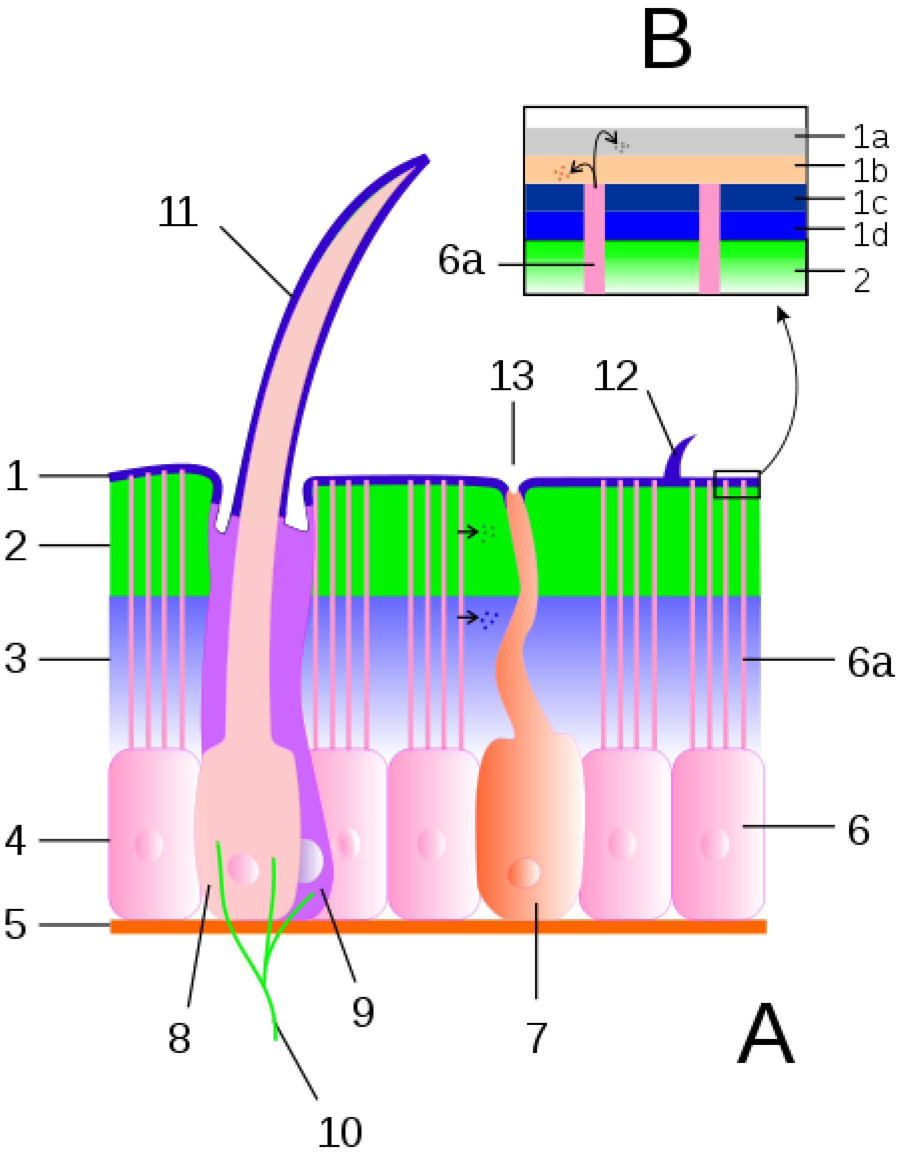
Arthropod Exoskeleton



The head of an ant: Chitin Type

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

Microscopic structure



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

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

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

Mechanical properties

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

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

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

Segmentation

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

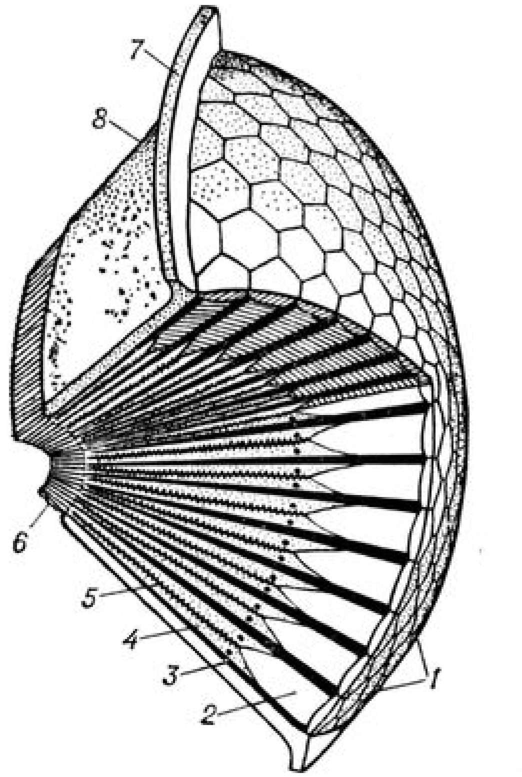
Ecdysis

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

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

Chapter- 2

Arthropod Eye



Anatomy of the compound eye of an insect

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

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

Eyes and functions

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

Genetic controls

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

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

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

Evolution

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

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

Origin

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

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

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

Trilobite eyes

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

Limulus

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

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

Insects & Crustaceans

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

Myriapods

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

Chapter- 3

Insect Flight

A Tau Emerald (*Hemicordulia tau*) dragonfly in flight

Insects are the only group of invertebrates known to have evolved flight. Insects possess some remarkable flight characteristics and abilities, still far superior to attempts by humans to replicate their capabilities. Even our understanding of the aerodynamics of flexible, flapping wings and how insects fly is imperfect. One application of this research is in the engineering of extremely small micro air vehicles with low Reynolds numbers.

Evolution and adaptation

Hoverfly in flight (*Xanthogramma pedissequum*)

Sometime in the Carboniferous Period, some 350 million years ago, when there were only two major land masses, insects began flying. How and why insect wings developed, however, is not well understood, largely due to the scarcity of appropriate fossils from the period of their development in the Lower Carboniferous. Three main theories on the origins of **insect flight** are that wings developed from paranotal lobes, extensions of the thoracic terga; that they are modifications of movable abdominal gills as found on aquatic naiads of mayflies; or that they developed from thoracic protrusions used as radiators.

Paranotal hypothesis

The paranotal hypothesis suggests that the insect's wings developed from paranotal lobes, a preadaptation found in insect fossils that is believed to have assisted stabilization while hopping or falling.

In favor of this hypothesis is the tendency of most insects, when startled while climbing on branches, to escape by dropping to the ground. Such lobes would have served as parachutes and enable the insect to land more softly.

The theory suggests that these lobes gradually grew larger and in a later stage developed a joint with the thorax. Even later would appear the muscles to move these crude wings. This model implies a progressive increase in the effectiveness of the wings, starting with parachuting, then gliding and finally active flight.

Still, lack of substantial fossil evidence of the development of the wing joints and muscles poses a major difficulty to the theory, as does the seemingly spontaneous development of articulation and venation, and it has been largely rejected by experts in the field.

Epicoxal hypothesis

Some entomologists have suggested that a possible origin for insect wings might have been the movable abdominal gills found in many aquatic insects, such as on naiads of mayflies. According to this theory these tracheal gills, which started their way as exits of the respiratory system and over time were modified into locomotive purposes, eventually developed into wings. The tracheal gills are equipped with little winglets that perpetually vibrate and have their own tiny straight muscles.

Endite-exite hypothesis

The hypothesis with perhaps the strongest evidence is that which stems from the adaptation of endites and exites, appendages on the respective inner and outer aspects of the primitive arthropod limb. This was advanced by Trueman based on a study by Goldschmidt in 1945 on *Drosophila melanogaster*, in which a *pod* variation displayed a mutation transforming normal wings to what was interpreted as a triple-jointed leg arrangement with some additional appendages but lacking the tarsus, where the wing's costal surface normally would be. This mutation was reinterpreted as strong evidence for a dorsal exite and endite fusion, rather than a leg, with the appendages fitting in much better with this hypothesis. The innervation, articulation and musculature required for the evolution of wings are already present in podomeres.

Other hypotheses

Suggestions have been made that wings may have evolved initially for sailing on the surface of water as seen in some stoneflies. An alternative idea is that it drives from directed aerial gliding descent—a preflight phenomena found in some apterygote, a wingless sister taxa to the winged insects.

The earliest fliers were similar to dragonflies with two sets of wings, direct flight muscles, and no ability to fold their wings over their abdomens. Most insects today, which evolved from those first fliers, have simplified to either one pair of wings or two pairs functioning as a single pair and using a system of indirect flight muscles.

Natural selection has played an enormous role in refining the wings, control and sensory systems, and anything else that affects aerodynamics or kinematics. One noteworthy trait is wing twist. Most insect wings are twisted, as are helicopter blades, with a higher angle of attack at the base. The twist generally is between 10 and 20 degrees. In addition to this twist, the wing surfaces are not necessarily flat or featureless; most larger insects have wing membranes distorted and angled between the veins in such a way that the cross-section of the wings approximates an airfoil. Thus, the wing's basic shape already is capable of generating a small amount of lift at zero angle of attack. Most insects control their wings by adjusting tilt, stiffness, and flapping frequency of the wings with tiny muscles in the thorax (below). Some insects evolved other wing features that are not advantageous for flight, but play a role in something else, such as mating or protection.

Some insects, occupying the biological niches that they do, need to be incredibly maneuverable. They must find their food in tight spaces and be capable of escaping larger predators - or they may themselves be predators, and need to capture prey. Their maneuverability, from an aerodynamic viewpoint, is provided by high lift and thrust forces. Typical insect fliers can attain lift forces up to three times their weight and horizontal thrust forces up to five times their weight. There are two substantially different insect flight mechanisms, and each has its own advantages and disadvantages - just because odonates have a more primitive flight mechanism does not mean they are less able fliers; they are, in certain ways, more agile than anything that has evolved afterward.

Direct flight mechanism

Unlike most other insects, the wing muscles of mayflies and odonates (the two living orders traditionally classified as "Paleoptera") insert directly at the wing bases, which are hinged so that a small movement of the wing base downward, lifts the wing itself upward, very much like rowing through the air. In mayflies, the hind wings are reduced, sometimes absent, and play little role in their flight, which is not particularly agile or graceful. In contrast, even though dragonflies cannot hover in still air with this primitive mechanism (although, with careful use of wind currents, they can remain nearly stationary), damselflies can, and in both groups, the fore and hind wings are similar in shape and size, and operated independently, which gives a degree of fine control and mobility in terms of the abruptness with which they can change direction and speed, not seen in other flying insects. This is not surprising, given that odonates are all aerial predators, and they have always hunted other airborne insects - evolutionary pressures have led to more advanced flight ability.

Indirect flight mechanism

Rare buzz pollination of parsley by a honeybee

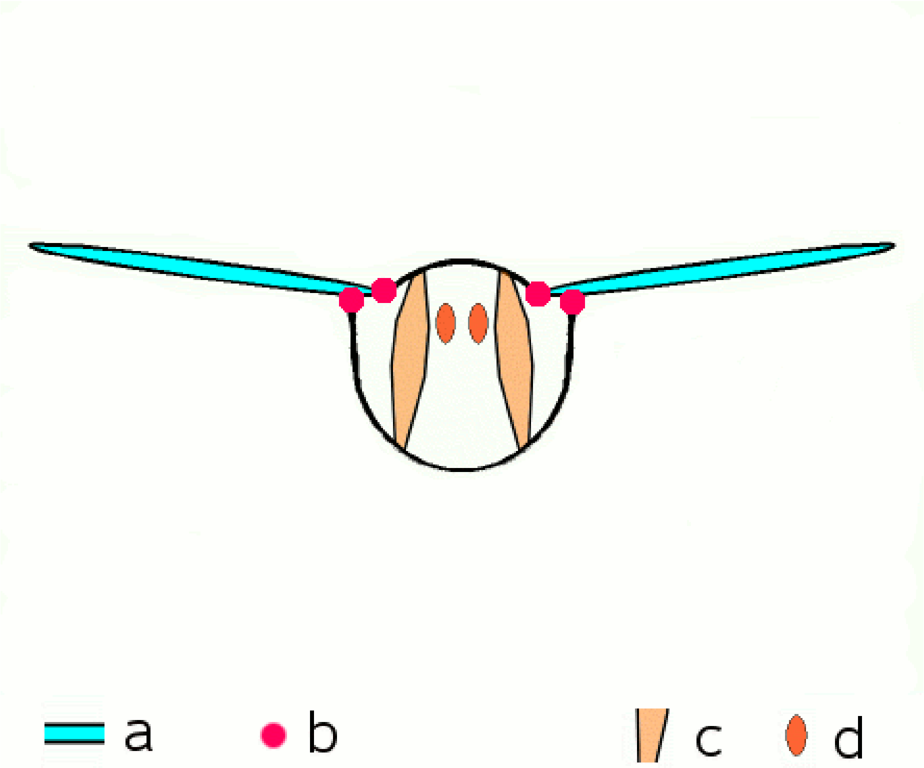
Other than the two orders with direct flight muscles, all other living winged insects fly using a different mechanism, involving indirect flight muscles. This mechanism evolved once, and is the defining feature (synapomorphy) for the infraclass Neoptera; it corresponds, probably not coincidentally, with the appearance of a wing-folding mechanism, which allows Neopteran insects to fold the wings back over the abdomen when at rest (though this ability has been lost secondarily in some groups, such as all butterflies).

In the higher groups with two functional pairs of wings, both pairs are linked together mechanically in various ways, and function as a single wing, although this is not true in the more primitive groups. What all Neoptera share, however, is the way the muscles in the thorax work: these muscles, rather than attaching to the wings, attach to the thorax and deform it; since the wings are extensions of the thoracic exoskeleton, the deformations of the thorax cause the wings to move as well. A set of **dorsal longitudinal muscles** compress the thorax from front to back, causing the dorsal surface of the thorax (notum) to bow upward, making the wings flip down. A set of **tergosternal muscles** pull the notum downward again, causing the wings to flip upward.

In a few groups, the downstroke is accomplished solely through the elastic recoil of the thorax when the tergosternal muscles are relaxed. Several small sclerites at the wing base have other, separate, muscles attached and these are used for fine control of the wing base in such a way as to allow various adjustments in the tilt and amplitude of the wing beats.

One of the final refinements that has appeared in some of the higher Neoptera (Coleoptera, Diptera, and Hymenoptera) is a type of muscular or neural control system whereby a single nerve impulse causes a muscle fiber to contract multiple times; this allows the frequency of wing beats to exceed the rate at which the nervous system can send impulses. This specialized form of muscle is termed **asynchronous flight muscle**. The overall effect is that many higher Neoptera can hover, fly backward, and perform other feats involving a degree of fine control that insects with direct flight muscles cannot achieve.

Basic aerodynamics



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

There are two basic aerodynamic models of insect flight. Most insects use a method that creates a spiralling leading edge vortex. These flapping wings move through two basic half-strokes. The downstroke starts up and back and is plunged downward and forward. Then the wing is quickly flipped over, supination, so that the leading edge is pointed backward. The upstroke then pushes the wing upward and backward. Then the wing is flipped again, pronation, and another downstroke can occur. The frequency range in insects with synchronous flight muscles typically is 5 to 200 hertz (Hz). In those with asynchronous flight muscles, wing beat frequency may exceed 1000 Hz. When the insect is hovering, the two strokes take the same amount of time. A slower downstroke, however, provides thrust.

Identification of major forces is critical to understanding insect flight. The first attempts to understand flapping wings assumed a quasi-steady state. This means that the air flow over the wing at any given time was assumed to be the same as how the flow would be over a non-flapping, steady-state wing at the same angle of attack. By dividing the flapping wing into a large number of motionless positions and then analysing each position, it would be possible to create a timeline of the instantaneous forces on the wing at every moment. The calculated lift was found to be too small by a factor of three, so researchers realised that there must be unsteady phenomena providing aerodynamic forces. There were several developing analytical models attempting to approximate flow close to a flapping wing. Some researchers predicted force peaks at supination. With a dynamically scaled model of a fruit fly, these predicted forces later were confirmed. Others argued that the force peaks during supination and pronation are caused by an unknown rotational effect that fundamentally is different from the translational phenomena. There is some disagreement with this argument. Through computational fluid dynamics, some researchers argue that there is no rotational effect. They claim that the high forces are caused by an interaction with the wake shed by the previous stroke.

Similar to the rotational effect mentioned above, the phenomena associated with flapping wings are not completely understood or agreed upon. Because every model is an approximation, different models leave out effects that are presumed to be negligible. For example, the *Wagner effect* says that circulation rises slowly to its steady-state due to viscosity when an inclined wing is accelerated from rest. This phenomenon would explain a lift value that is less than what is predicted. Typically, the case has been to find sources for the added lift. It has been argued that this effect is negligible for flow with a Reynolds number that is typical of insect flight. The Wagner effect was ignored, consciously, in at least one recent model.

One of the most important phenomena that occurs during insect flight is leading edge suction. This force is significant to the calculation of efficiency. The concept of leading edge suction first was put forth to describe vortex lift on sharp-edged delta wings. At high angles of attack, the flow separates over the leading edge, but reattaches before reaching the trailing edge. Within this bubble of separated flow is a vortex. Because the angle of attack is so high, a lot of momentum is transferred downward into the flow. These two features create a large amount of lift force as well as some additional drag. The important feature, however, is the lift. Because the flow has separated, yet it still provides large amounts of lift, this phenomenon is called *stall delay*. This effect was observed in flapping insect flight and it was proven to be capable of providing enough lift to account for the deficiency in the quasi-steady-state models. This effect is used by canoeists in a sculling draw stroke.

All of the effects on a flapping wing may be reduced to three major sources of aerodynamic phenomena: the leading edge vortex, the steady-state aerodynamic forces on the wing, and the wing's contact with its wake from previous strokes.

The size of flying insects ranges from about 20 micrograms to about 3 grams. As insect body mass increases, wing area increases and wing beat frequency decreases. For larger insects, the Reynolds number (Re) may be as high as 10000. For smaller insects, it may be as low as 10. This means that viscous effects are much more important to the smaller insects, although the flow is still laminar, even in the largest fliers.

Another interesting feature of insect flight is the body tilt. As flight speed increases, the insect body tends to tilt nose-down and become more horizontal. This reduces the frontal area and therefore, the body drag. Since drag also increases as forward velocity increases, the insect is making its flight more efficient as this efficiency becomes more necessary. Additionally, by changing the geometric angle of attack on the downstroke, the insect is able to keep its flight at an optimal efficiency through as many manoeuvres as possible.

The development of general thrust is relatively small compared with lift forces. Lift forces may be more than three times the insect's weight, while thrust at even the highest speeds may be as low as 20% of the weight. This force is developed primarily through the less powerful upstroke of the flapping motion.

The second method of flight, fling and clap, functions differently. In this process, the wings clap together above the insect's body and then fling apart. As they fling open, the air gets sucked in and creates a vortex over each wing. This bound vortex then moves across the wing and, in the clap, acts as the starting vortex for the other wing. By this effect, circulation and thus, lift are increased to the extent of being higher, in most cases, than the typical leading edge vortex effect. One of the reasons this method is not employed by more insects is the expected damage and wear to the wings caused by the repeated clapping. It is prevalent, however, among insects that are very small and experience low Reynolds numbers.

Wing coupling

"Oiketicus" spp. (Family Psychidae). The frenulum can be seen at the top of the rear wing, which hooks onto the retinaculum so that the wings travel together during flight. Magnification: 10x

Some four-winged insect orders, such as the Lepidoptera, have developed a wide variety of morphological wing-coupling mechanisms in the imago which render these taxa as "functionally dipterous". All, but the most basal forms, exhibit this wing-coupling.

The mechanisms are of three different types - jugal, frenulo-retinacular and amplexiform.

The more primitive groups have an enlarged lobe-like area near the basal posterior margin, i.e. at the base of the forewing, called *jugum*, that folds under the hindwing in flight.

Other groups have a frenulum on the hindwing that hooks under a retinaculum on the forewing.

In the butterflies (except the male of one species of hesperiid) and in the Bombycoidea (except the Sphingidae), there is no arrangement of frenulum and retinaculum to couple the wings. Instead, an enlarged humeral area of the hindwing is broadly overlapped by the forewing. Despite the absence of a specific mechanical connection, the wings overlap and operate in phase. The power stroke of the forewing pushes down the hindwing in unison. This type of coupling is a variation of frenate type but where the frenulum and retinaculum are completely lost.

Biochemistry

The biochemistry of insect flight has been a focus of considerable study. While many insects use carbohydrates and lipids as the energy source for flight, many beetles and flies prefer to use the amino acid, proline, as their energy source. Some species also use a combination of sources and moths, such as *Manduca sexta*, prefer to use carbohydrates for pre-flight warm-up.

Chapter- 4

Evolution of Insects

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

Insects are a highly diverse group of organisms with a worldwide distribution. They have conquered every terrestrial environment and have complex interactions with a wide variety of organisms, including predatory-prey relationships.

Taxonomic Affinities

The relationships of insects to other animal groups remain unclear. Although more traditionally grouped with millipedes and centipedes, evidence has emerged favouring closer evolutionary ties with the crustaceans. In the Pancrustacea theory, insects, together with among others Malacostraca, make up a monophyletic group (sharing a common ancestor): this is today a well accepted hypothesis.

Early evidence

The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, estimated at 396-407 million years old. This species already possessed dicondylic mandibles, a feature associated with winged insects, suggesting that wings may already have evolved at this time. Thus, the first insects probably appeared earlier, in the Silurian period.

The subclass Apterygota (wingless insects) is now considered artificial as the silverfish (order Thysanura) are more closely related to Pterygota (winged insects) than to bristletails (order Archaeognatha). For instance, just like flying insects, Thysanura have so-called dicondylic mandibles, while Archaeognatha have monocondylic mandibles. The reason for their resemblance is not due to a particularly close relationship, but rather because they both have kept a primitive and original anatomy in a much higher degree than the winged insects. The most primitive order of flying insects, the mayflies (Ephemeroptera), are also those who are most morphologically and physiologically similar to these wingless insects. Some mayfly nymphs resemble aquatic thysanurans.

Modern Archaeognatha and Thysanura still have rudimentary appendages on their abdomen called styli, while more primitive and extinct insects known as Monura had much more developed abdominal appendages, as seen here. The abdominal and thoracic segments in the earliest terrestrial ancestor of the insects would have been more similar to each other than they are today, and the head had well developed compound eyes and long antennae. Their body size is not known yet. As the most primitive group today, Archaeognatha, is most abundant near the coasts, it could mean that this was the kind of habitat where the insect ancestors became terrestrial. But this specialization to coastal niches could also have a secondary origin, just as could their jumping locomotion, as it is the crawling Thysanura who are considered to be most original (plesiomorphic). By looking at how primitive cheliceratan book gills (still seen in horseshoe crabs) evolved into book lungs in primitive spiders and finally into tracheae in more advanced spiders (most of them still have a pair of book lungs intact as well), it is possible the trachea of insects was formed in a similar way, modifying gills at the base of their appendages.

So far there is nothing that suggests the insects were a particularly successful group of animals before they got their wings.

Odonata

The Odonata (dragonflies) are also a good candidate as the oldest living member of the Pterygota. Mayflies are morphologically and physiologically more primitive, but the derived and advanced characteristics of dragonflies could have evolved independently in their own direction for a long time. It seems that orders with aquatic nymphs or larvae become evolutionarily conservative once they had adapted to water. If mayflies made it to the water first, this could partly explain why they are more primitive than dragonflies, even if dragonflies have an older origin.

Similarly, stoneflies are the most primitive of the Neoptera, but they were not necessarily the first order to branch off. This also makes it less likely that an aquatic ancestor would have the evolutionary potential to give rise to all the different forms and species of insects that we know today.

Dragonfly nymphs have a unique labial "mask" used for catching prey, and the imago has a unique way of copulating, using a secondary male sex organ on the second abdominal segment. It looks like abdominal appendages modified for sperm transfer and direct insemination have occurred at least twice in insect evolution, once in Odonata and once in the other flying insects. If these two different methods are the original ways of copulating for each group, it is a strong indication that it is the dragonflies who are the oldest, not the mayflies. There is still not agreement about this. Another scenario is that abdominal appendages adapted for direct insemination have evolved three times in insects; once Odonata, once in mayflies and once in the Neoptera, both mayflies and Neoptera choosing the same solution. If so, it is still possible that mayflies are the oldest order among the flying insects. The power of flight is assumed to have evolved only once, suggesting sperm transfer in the earliest flying insects still was done indirectly.

One possible scenario on how direct insemination evolved in insects is seen in scorpions. The male deposits a spermatophore on the ground, locks its claws with the female's claws and then guides her over his packet of sperm, making sure it comes in contact with her genital opening.

When the early (male) insects laid their spermatophores on the ground, it seems likely that some of them used the clasping organs at the end of their body to drag the female over the package. The ancestors of Odonata evolved the habit of grabbing the female behind her head, as they still do today. This action, rather than not grasping the female at all, would have increased the male's chances of spreading its genes. The chances would be further increased if they first attached their spermatophore safely on their own abdomen before they placed their abdominal claspers behind the female's head; the male would then not let the female go before her abdomen had made direct contact with his sperm storage, allowing the transfer of all sperm.

This also meant increased freedom in searching for a female mate because the males could now transport the packet of sperm elsewhere if the first female slipped away. This ability would eliminate the need to either wait for another female at the site of the deposited sperm packet or to produce a new packet, wasting energy. Other advantages include the possibility of mating in other, safer places than flat ground, such as in trees or bushes.

If the ancestors of the other flying insects evolved the same habit of clasping the female and dragging her over their spermathophore, but posterior instead of anterior like the Odonata does, their genitals would come very close to each others. And from there on, it would be a very short step to modify the vestigial appendages near the male genital opening to transfer the sperm directly into the female. The same appendages the male Odonata use to transfer their sperm to their secondary sexual organs at the front of their abdomen.

All insects with an aquatic nymphal or larval stage seem to have adapted to water secondarily from terrestrial ancestors. Of the most primitive insects with no wings at all, Archaeognatha and Thysanura, all members live their entire life cycle in terrestrial environments. As mentioned previously, Archaeognatha were the first to split off from the branch that led to the winged insects (Pterygota), and then the Thysanura branched off. This indicates that these three groups (Archaeognatha, Thysanura and Pterygota) have a common terrestrial ancestor, which probably resembled a primitive model of Apterygota, was an opportunistic generalist and laid spermatophores on the ground instead of copulating, like Thysanura still do today. If it had feeding habits similar to the majority of apterygotes of today, it lived mostly as a decomposer.

One should expect that a gill breathing arthropod would modify its gills to breathe air if it were adapting to terrestrial environments, and not evolve new respiration organs from bottom up next to the original and still functioning ones.

Then comes the fact that insect (larva and nymph) gills are actually a part of a modified, closed trachea system specially adapted for water, called tracheal gills. The arthropod trachea can only arise in an atmosphere and as a consequence of the adaptations of living on land. This too indicates that insects are descended from a terrestrial ancestor.

And finally when looking at the three most primitive insects with aquatic nymphs (called naiads: Ephemeroptera, Odonata and Plecoptera), each order has its own kind of tracheal gills that are so different from one another that they must have separate origins. This would be expected if they evolved from land-dwelling species.

This means that one of the most interesting parts of insect evolution is what happened between the Thysanura-Pterygota split and the first flight.

Origin of insect flight

The origin of insect flight remains obscure, since the earliest winged insects currently known appear to have been capable fliers. Some extinct insects (e.g. the Palaeodictyoptera) had an additional pair of winglets attached to the first segment of the thorax, for a total of three pairs.

The wings themselves are thought by many to be highly modified (tracheal) gills. And there is no doubt that the tracheal gills of the mayfly nymph in many species look like wings. By comparing a well developed pair of gill blades in the naiads and a reduced pair of hind wings on the adults, it is not hard to imagine that the mayfly gills (tergaliae) and insect wings have a common origin, and newer research also supports this. The tergaliae are not found in any other order of insects, and they have evolved in different directions with time. In some nymphs/naiads the most anterior pair has become sclerotized and works as a gill cover for the rest of the gills. Others can form a large sucker, be used for swimming or modified into other shapes. But it doesn't have to mean that these structures were originally gills. It could also mean that the tergaliae evolved from the same structures which gave rise to the wings, and that flying insects evolved from a wingless terrestrial species with pairs of plates on its body segments: three on the thorax and nine on the abdomen (mayfly nymphs with nine pairs of tergaliae on the abdomen exist, but so far no living or extinct insects with plates on the last two segments have been found). If these were primary gills, it would be a mystery why they should have waited so long to be modified when we see the different modifications in modern mayfly nymphs.

Theories

When the first forests arose on Earth, new niches for terrestrial animals were created. Spore-feeders and others who depended on plants and/or the animals living around them would have to adapt too to make use of them. In a world with no flying animals, it would probably just be a matter of time before some arthropods who were living in the trees evolved paired structures with muscle attachments from their exoskeleton and used them for gliding, one pair on each segment. Further evolution in this direction would give bigger gliding structures on their thorax and gradually smaller ones on their abdomen. Their bodies would have become stiffer while thysanurans, which didn't evolve flight, kept their flexible abdomen.

Mayfly nymphs must have adapted to water while they still had the "gliders" on their abdomen intact. So far there is no concrete evidence to support this theory either, but it is one that offers an explanation for the problems of why presumably aquatic animals evolved in the direction they did.

Leaping and arboreal insects seems like a good explanation for this evolutionary process for several reasons. Because early winged insects were lacking the sophisticated wing folding mechanism of neopterous insects, they must have lived in the open and not been able to hide or search for food under leaves, in cracks, under rocks and other such confined spaced. In these old forests there weren't many open places where insects with huge structures on their back could have lived without experiencing huge disadvantages. If insects got their wings on land and not in water, which clearly seems to be the case, the tree canopies would be the most obvious place where such gliding structures could have emerged, in a time when the air was a new territory. The question is if the plates used for gliding evolved from "scratch" or by modifying already existing anatomical details. The thorax in Thysanura and Archaeognatha are known to have some structures connected to their trachea which share similarities to the wings of primitive insects. This suggests the origin of both the wings and the spiracles are related.

Gliding requires universal body modifications, as seen in present-day vertebrates such as some rodents and marsupials, which have grown wide, flat expansions of skin for this purpose. The flying dragons (genus *Draco*) of Indonesia has modified its ribs into gliders, and even some snakes can glide through the air by spreading their ribs. The main difference is that while vertebrates have an inner skeleton, primitive insects had a flexible and adaptive exoskeleton.

It is clear that there would have been some animals living in the trees, as animals are always taking advantage of all available niches, both for feeding and protection. At the time, the reproductive organs were by far the most nutritious part of the plant, and these early plants show signs of arthropod consumption and adaptations to protect themselves, for example by placing their reproductive organs as high up as possible. But there will always be some species who will be able to cope with that by following the their food source up the trees.

Knowing that insects were terrestrial at that time and that some arthropods (like primitive insects) were living in the tree crowns, it seems less likely that they would have developed their wings down on the ground or in the water.

In a three dimensional environment such as trees, the ability to glide would increase the insects' chances to survive a fall, as well as saving energy. This trait has repeated itself in modern wingless species such as the gliding ants who are living an arboreal life. When the gliding ability first had originated, gliding and leaping behavior would be a logical next step, which would eventually be reflected in their anatomical design.

The need to navigate through vegetation and to land safely would mean good muscle control over the proto-wings, and further improvements would eventually lead to true (but primitive) wings.

While the thorax got the wings, a long abdomen could have served as a stabilizer in flight.

It is also worth remembering that some of the earliest flying insects were large predators. This isn't surprising since there weren't yet any other predators hunting in the air: it was therefore a totally new ecological niche. Some of the prey were without a doubt other insects, as insects with proto-wings would have radiated into other species even before the wings were fully evolved. From this point onwards, the arms race could continue: the same predator/prey co-evolution which has existed as long as there have been predators and prey on earth; both the hunters and the hunted were in need of improving and extending their flight skills even further to keep up with the other.

Insects that had evolved their proto-wings in a world without flying predators could afford to be exposed openly without risk, but this changed when carnivorous flying insects evolved. It is unknown when they first evolved, but once these predators had emerged they put a strong selection pressure on their victims and themselves. Those of the prey who came up with a good solution about how to fold their wings over their backs in a way that made it possible for them to live in narrow spaces would not only be able to hide from flying predators (and terrestrial predators if they were on the ground) but also to exploit a wide variety of niches that were closed to those who couldn't fold their wings in this way. And today the neopterous insects (those that can fold their wings back over the abdomen) are by far the most dominant group of insects.

The water-skimming theory suggests that skimming on the water surface is the origin of insect flight. This theory is based on the fact that the first fossil insects, the Devonian *Rhyniognatha hirsti*, is thought to have possessed wings, even though the insects closest evolutionary ties are with crustaceans, which are aquatic.

Life cycle

Mayflies

Another primitive trait of the mayflies are the subimago; no other insects have this winged yet sexually immature stage. A few specialized species have females with no subimago, but retain the subimago stage for males.

The reasons the subimago still exists in this order could be that there hasn't been enough selection pressure to get rid of it; it also seems specially adapted to do the transition from water to air.

The male geniatalia are not fully functional at this point. One reason for this could be that the modification of the abdominal appendages into male copulation organs emerged later than the evolution of flight. This is indicated by the fact that dragonflies have a different copulation organ than other insects.

As we know, in mayflies the nymphs and the adults are specialized for two different ways of living; in the water and in the air. The only stage (instar) between these two is the subimago. In more primitive fossil forms, the preadult individuals had not just one instar but numerous ones (while the modern subimago do not eat, older and more primitive species with a subimagos were probably feeding in this phase of life too as the lines between the instars were much more diffuse and gradual than today). Adult form was reached several moults before maturity. They probably didn't have more instars after becoming fully mature. This way of maturing is how Apterygota do it, which moult even when mature, but not winged insects.

Modern mayflies have eliminated all the instars between imago and nymph, except the single instar called subimago, which is still not (at least not in the males) fully sexually mature. The other flying insects with incomplete metamorphosis (Exopterygota) have gone a little further and completed the trend; here all the immature structures of the animal from the last nymphal stage are completed at once in a single final moult. The more advanced insects with larvae and complete metamorphosis (Endopterygota) have gone even further. An interesting theory here is that the pupal stage is actually a strongly modified and extended stage of subimago, but so far it is nothing more than a theory. Interestingly enough there are some insects within the Exopterygota, thrips and whiteflies (Aleyrodidae), who have evolved pupae-like stages too.

Distant ancestors

The distant ancestor of flying insects, a species with primitive proto-wings, had a more or less ametabolous life cycle and instars of basically the same type as thysanurans with no defined nymphal, subimago or adult stages as the individual became older. Individuals developed gradually as they were growing and moulting, but there were probably no big changes in between instars.

Modern mayfly nymphs do not acquire gills until after their first moult. Before this stage they are so small that there is no need for gills to extract oxygen from the water. This could be a trait from the common ancestor all flyers evolved from. An early terrestrial insect would have no need for paired outgrowths from the body before it started to live in the trees (or in the water, for that matter), so it would not have any.

This would also affect the way their offspring looked like in the early instars, resembling earlier ametabolous generations even after they had started to adapt to a new way of living, in a habitat where they actually could have some good use for flaps along their body. Since they matured in the same way as thysanurans with plenty of moultings as they were growing and very little difference between the adults and much younger individuals (unlike modern insects, who are hemimetabolous or holometabolous), there probably wasn't much room for adapting into different niches depending on age and stage. Also, it would have been difficult for an animal already adapted to a niche to make a switch to a new niche later in life based on age or size differences alone when these differences were not significant.

So they had to specialize and focus their whole existence on improving a single lifestyle in a particular niche. The older the species and the single individuals became, the more would they differ from their original form as they adapted to their new lifestyle better than the generations before. The final body design was no longer achieved while still inside the egg, but continued to develop for most of the life, causing a bigger difference between the youngest and oldest individuals. Assuming that mature individuals most likely mastered their new element better than did the nymphs who had the same lifestyle, it would appear to be an advantage if the immatures reached adult shape and form as soon as possible. This may explain why they evolved fewer but more intense instars and a stronger focus on the adult body, and the differences between the adults and the first instars were greater, instead of just gradually growing bigger as earlier generations had done. This evolutionary trend explains how they went from ametabolous to hemimetabolous insects.

Reaching maturity and a fully grown body became only a part of the development process, gradually also a new anatomy and new abilities only possible in the later stages of life, were included. The anatomy they were born and grew up with had limitations the adults who had learned to fly didn't have. If they couldn't live their early life the way adults did, immature individuals had to adapt to the best way of living and surviving despite their limitations till the moment came when they could leave them behind. This would be a starting point in the evolution where imago and nymphs started to live in different niches, some more clearly defined than others. Also, a final anatomy, size and maturity reached at once with a single final nymphal stage meant less waste of time and energy, and also made a more complex adult body structure. These strategies obviously became very successful with time.

Late Carboniferous and Early Permian insect orders include both several current very long-lived groups (mayflies, (Ephemeroptera), dragonflies (Odonata), cockroaches (Blattodea), and Orthoptera (grasshoppers and their relatives)) and a number of Paleozoic forms. During this era, some giant dragonfly-like forms – e.g. *Meganeura* and *Meganeuropsis* (Order Protodonata) and *Mazothairos* (Order Palaeodictyoptera) – reached wingspans of 55 to 70 cm (22 to 28 in), making them far larger than any living insect. Also their nymphs must have had a very impressive size. This gigantism may have been due to higher atmospheric oxygen levels (up to 80% above modern levels during the Carboniferous) that allowed increased respiratory efficiency relative to today. The lack of flying vertebrates could have been another factor.

Most extant orders of insects developed during the Permian period that began around 270 million years ago. Many of the early groups became extinct during the Permian-Triassic extinction event, the largest mass extinction in the history of the Earth, around 252 million years ago.

The remarkably successful Hymenopterans appeared in the Cretaceous but achieved their diversity more recently, in the Cenozoic. A number of highly successful insect groups — especially the Hymenoptera and Lepidoptera (butterflies), as well as many types of Diptera (flies) and Coleoptera (beetles) — evolved in conjunction with flowering plants, a powerful illustration of co-evolution.

Many modern insect genera developed during the Cenozoic; insects from this period on are often found preserved in amber, often in perfect condition. Such specimens are easily compared with modern species. The study of fossilized insects is called paleoentomology.

Chapter- 5

Mollusc Shell

Closed and open shells of a marine bivalve, *Petricola pholadiformis*. A bivalve shell is composed of two hinged valves which are joined by a ligament.

Four views of a shell of the land snail *Arianta arbustorum*

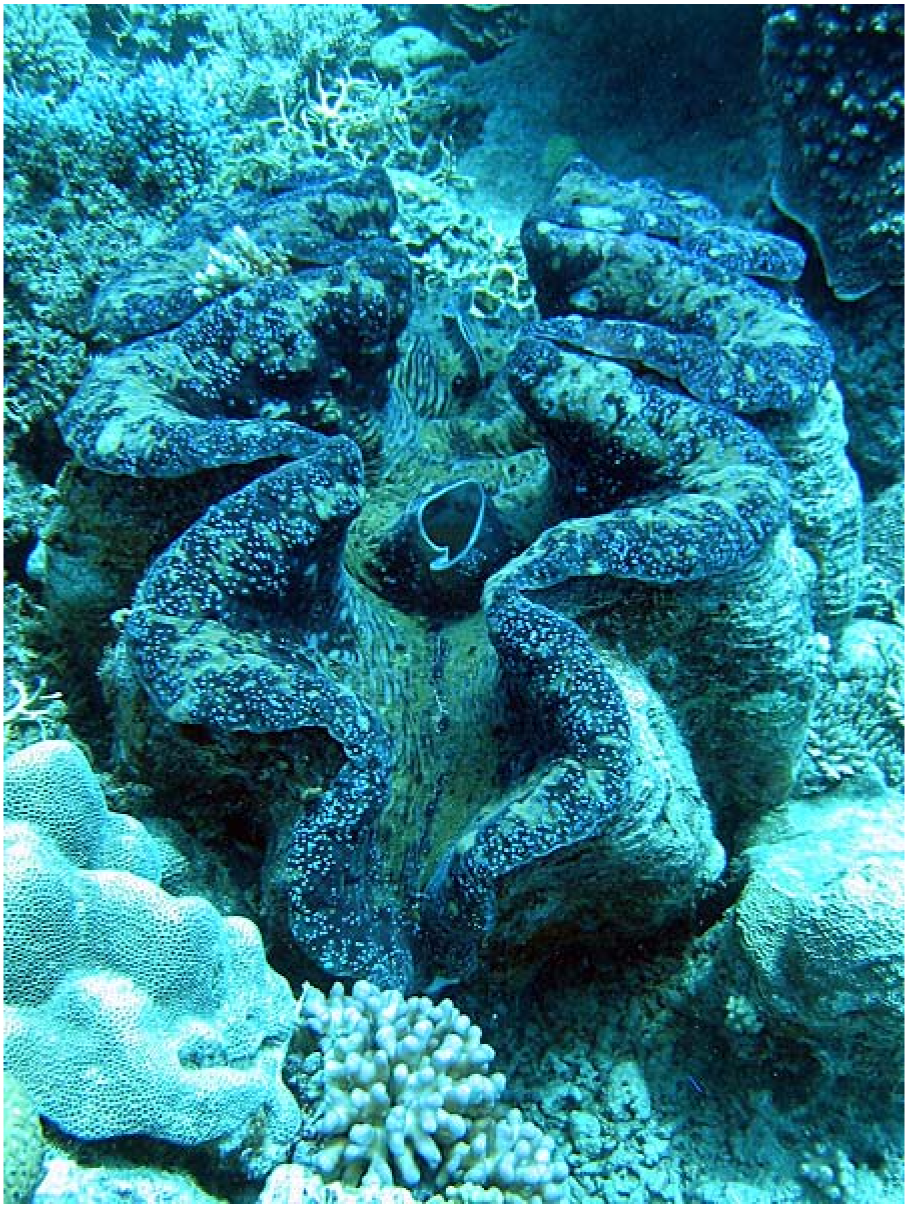
The **mollusc** (or **mollusk**) **shell** is typically a calcareous exoskeleton which encloses, supports and protects the soft parts of an animal in the phylum Mollusca, which includes snails, clams, tusk shells, and several other classes. Not all shelled molluscs live in the sea, many live on the land and in freshwater.

The ancestral mollusc is thought to have had a shell, but this has subsequently been lost or reduced on some families, such as the squid, octopus, and some smaller groups such as the caudofoveata and solenogastres, and the highly derived *Xenoturbella*. Today, over 100 000 living species bear a shell; there is some dispute as to whether these shell-bearing molluscs form a monophyletic group (conchifera) or whether shell-less molluscs are interleaved into their family tree.

Malacology, the scientific study of molluscs as living organisms, has a branch devoted to the study of shells, and this is called conchology - although these terms used to be, and to a minor extent still are, used interchangeably, even by scientists (this is more common in Europe).

Within some species of molluscs there is often a surprising degree of variation in the exact shape, pattern, ornamentation, and color of the shell.

Formation



The giant clam (*Tridacna gigas*) is the largest extant species of bivalve. The mantle is visible between the open valves

A mollusc shell is formed, repaired and maintained by a part of the anatomy called the mantle. Any injuries to or abnormal conditions of the mantle are usually reflected in the shape and form and even color of the shell. When the animal encounters harsh conditions that limit its food supply, or otherwise cause it to become dormant for a while, the mantle often ceases to produce the shell substance. When conditions improve again and the mantle resumes its task, a "growth line" is produced.

The mantle edge secretes a shell which has two components. The organic constituent is mainly made up of polysaccharides and glycoproteins; its composition may vary widely: some molluscs employ a wide range of chitin-control genes to create their matrix, whereas others just express one, suggesting that the role of chitin in the shell framework is highly variable; it may even be absent in monoplacophora. This organic framework controls the formation of calcium carbonate crystals, (never phosphate with the questionable exception of *Cobcrephora*), and dictates when and where crystals start and stop growing, and how fast they expand; it even controls the polymorph of the crystal deposited, controlling positioning and elongation of crystals and preventing their growth where appropriate.

The shell formation requires certain biological machinery. The shell is deposited within a small compartment, the extrapallial space, which is sealed from the environment by the periostracum, a leathery outer layer around the rim of the shell, where growth occurs. This caps of the extrapallial space, which is bounded on its other surfaces by the existing shell and the mantle. The periostracum acts as a framework from which the outer layer of carbonate can be suspended, but also, in sealing the compartment, allows the accumulation of ions in concentrations sufficient for crystallization to occur. The accumulation of ions is driven by ion pumps packed within the calcifying epithelium. Calcium ions are obtained from the organism's environment through the gills, gut and epithelium, transported by the haemolymph ("blood") to the calcifying epithelium, and stored as granules within or in-between cells ready to be dissolved and pumped into the extrapallial space when they are required. The organic matrix forms the scaffold that directs crystallization, and the deposition and rate of crystals is also controlled by hormones produced by the mollusc. Because the extrapallial space is supersaturated, the matrix could be thought of as impeding, rather than encouraging, carbonate deposition; although it does act as a nucleating point for the crystals and controls their shape, orientation and polymorph, it also terminates their growth once they reach the necessary size. Nucleation is endoepithelial in *Neopilina* and *Nautilus*, but exoepithelial in the bivalves and gastropods.

The formation of the shell involves a number of genes and transcription factors. On the whole, the transcription factors and signalling genes are deeply conserved, but the proteins in the secretome are highly derived and rapidly evolving. *engrailed* serves to demark the edge of the shell field; *dpp* controls the shape of the shell, and *Hox1* and *Hox4* have been implicated in the onset of mineralization. In gastropod embryos, *Hox1* is expressed where the shell is being accreted; however no association has been observed between *Hox* genes and cephalopod shell formation. Perlucin increases the rate at which calcium carbonate precipitates to form a shell when in saturated seawater; this protein is from the same group of proteins (C-type lectins) as those responsible for the formation of eggshell and pancreatic stone crystals, but the role of C-type lectins in mineralization is unclear. Perlucin operates in association with Perlustrin, a smaller relative of lustrin A, a protein responsible for the elasticity of organic layers that makes nacre so resistant to cracking. Lustrin A bears remarkable structural similarity to the proteins involved in mineralization in diatoms – even though diatoms use silica, not calcite, to form their tests!

Development

The shell-secreting area is differentiated very early in embryonic development. An area of the ectoderm thickens, then invaginates to become a "shell gland". The shape of this gland is tied to the form of the adult shell; in gastropods, it is a simple pit, whereas in bivalves, it forms a groove which will eventually become the hinge line between the two shells, where they are connected by a ligament. The gland subsequently evaginates in molluscs that produce an external shell. Whist invaginated, a periostracum - which will form a scaffold for the developing shell - is formed around the opening of the invagination, allowing the deposition of the shell when the gland is everted. A wide range of enzymes are expressed during the formation of the shell, including carbpnic anhydrase, alkaline phosphatase, and DOPA-oxidase (tyrosinase)/peroxidase.

The form of the molluscan shell is constrained by the organism's ecology. In molluscs whose ecology changes from the larval to adult form, the morphology of the shell also undergoes a pronounced modification at metamorphosis. The larval shell may have a completely different mineralogy to the adult conch, perhaps formed from amorphous calcite as opposed to an aragonite adult conch.

In those shelled molluscs that have indeterminate growth, the shell grows steadily over the lifetime of the mollusc by the addition of calcium carbonate to the leading edge or opening. Thus the shell gradually becomes longer and wider, in an increasing spiral shape, to better accommodate the growing animal inside. The shell thickens as it grows, so that it stays proportionately strong for its size.

Secondary loss

The loss of a shell in the adult form of some gastropods is achieved by the discarding of the larval shell; in other gastropods and in cephalopods, the shell is lost or demineralized by the resroption of its carbonate component by the mantle tissue.

Shell proteins

Hundreds of soluble and insoluble proteins, control shell formation. They are secreted into the extrapallial space by the mantle, which also secretes the glycoproteins, proteoglycans, polysaccharides and chitin that make up the organic shell matrix. Insoluble proteins tend to be thought of as playing a more important/major role in crystallization control. The organic matrix of shells tends to consist of β-chitin and silk fibroin. Perlucin encourages carbonate deposition, and is found at the interface of the chitinous and aragonitic layer in some shells. An acidic shell matrix appears to be essential to shell formation, in the cephalopods at least; the matrix in the non-mineralized squid gladius is basic.

In oysters and potentially most molluscs, the nacreous layer has an organic framework of the protein MSI60, which has a structure a little like spider silk and forms sheets; the prismatic layer uses MSI31 to construct its framework. This too forms beta-pleated sheets. Since acidic amino acids, such as aspartic acid and glutamic acid, are important mediators of biomineralization, shell proteins tend to be rich in these amino acids. Aspartic acid, which can make up up to 50% of shell framework proteins, is most abundant in calcitic layers, and also heavily present in aragonitic layers. Proteins with high proportions of glutamic acid are usually associated with amorphous calcium carbonate.

The soluble component of the shell matrix acts to inhibit crystallization when in its soluble form, but when it attaches to an insoluble substrate, it permits the nucleation of crystals. By switching from a dissolved to an attached form and back again, the proteins can produce 'bursts' of growth, producing the brick-wall structure of the shell.

Chemistry

The formation of a shell in molluscs appears to be related to the secretion of ammonia, which originates from urea. The presence of an ammonium ion raises the pH of the extrapallial fluid, favouring the deposition of calcium carbonate. This mechanism has been proposed not only for molluscs, but also for other unrelated mineralizing lineages.

Structure

The calcium carbonate layers in a shell are generally of two types: an outer, chalk-like prismatic layer and an inner pearly, lamellar or nacreous layer. The layers usually incorporate a substance called conchiolin, often in order to help bind the calcium carbonate crystals together. Conchiolin is composed largely of quinone-tanned proteins.

The periostracum and prismatic layer are secreted by a marginal band of cells, so that the shell grows at its outer edge. Conversely, the nacreous layer is derived from the main surface of the mantle.

Some shells contain pigments which are incorporated into the structure. This is what accounts for the striking colors and patterns that can be seen in some species of seashells, and the shells of some tropical land snails. These shell pigments sometimes include compounds such as pyrroles and porphyrins.

Shells are almost always composed of polymorphs of calcium carbonate - either calcite or aragonite. In many cases, such as the shells of many of the marine gastropods, different layers of the shell are composed of calcite and aragonite. In a few species which dwell near hydrothermal vents, iron sulfide is used to construct the shell. Phosphate is never utilised by molluscs, with the exception of *Cobcrephora*, whose molluscan affinity is uncertain.

Shells are composite materials of calcium carbonate (found either as calcite or aragonite) and organic macromolecules (mainly proteins and polysaccharides.) Shells can have numerous ultrastructural motifs, the most common being crossed-lamellar (aragonite), prismatic (aragonite or calcite), homogeneous (aragonite), foliated (aragonite) and nacre (aragonite). Although not the most common, nacre is the most studied type of layer. Shells of the class Polyplacophora are made of aragonite.

Size

In most shelled molluscs, the shell is large enough for all of the soft parts to be retracted inside when necessary, for protection from predation or from desiccation. However there are many species of gastropod mollusc in which the shell is somewhat reduced or considerably reduced, such that it offers some degree of protection only to the visceral mass, but is not large enough to allow the retraction of the other soft parts. This is particularly common in the opisthobranchs and in some of the pulmonates.

Some gastropods have no shell at all, or only an internal shell or internal calcareous granules, and these species are often known as slugs. Semislugs are pulmonate slugs with a greatly reduced external shell which is in some cases partly covered by the mantle.

Shape

The shape of the molluscan shell is controlled both by transcription factors (such as engrailed and decapentaplegic) and by developmental rate. The simplification of a shall form is thought to be relatively easily evolved, and many gastrtopod lineages have independently lost the complex coiled shape. However, re-gaining the coiling requires many morphological modifications and is much rarer. Despite this, it can still be accomplished; it is known from one lineage that was uncoiled for at least 20 million years, before modifying its developmental timing to restore the coiled morphology.

In bivalves at least, the shape does change through growth, but the pattern of growth is constant. At each point around the aperture of the shell, the rate of growth remains constant. This results in different areas growing at different rates, and thus a coiling of the shell and a change in its shape - its convexity, and the shape of the opening - in a predictable and consistent fashion.

The shape of the shell has an environmental as well as a genetic component; clones of gastropods can exert different shell morphologies. Indeed intra-species variation can be many times larger than inter-species variation.

Evolution

The fossil record shows that all molluscan classes evolved from a shelled ancestor looking something like a modern monoplacophoran, and that modifications of the shell form ultimately led to the formation of new classes and lifestyles. However, a growing body of molecular and biological data indicates that at least certain shell features have evolved many times, independently. The nacreous layer of shells is a complex structure, but rather than being difficult to evolve, it has in fact arisen many times convergently. The genes used to control its formation vary greatly between taxa: under 10% of the (non-housekeeping) genes expressed in the shells that produce gastropod nacre are also found in the equivalent shells of bivalves: and most of these shared genes are also found in mineralizing organs in the deuterostome lineage. The independent origins of this trait are further supported by crystallographic differences between clades: the orientation of the axes of the deposited aragonite 'bricks' that make up the nacreous layer is different in each of the monoplacophora, gastropods and bivalves.

Mollusc shells (especially those formed by marine species) are very durable and outlast the otherwise soft-bodied animals that produce them by a very long time (sometimes thousands of years even without being fossilized). Most shells of marine molluscs fossilize rather easily, and fossil mollusc shells date all the way back to the Cambrian period. Large amounts of shells sometimes form sediment, and over a geological time span can become compressed into limestone deposits.

Most of the fossil record of molluscs consists of their shells, since the shell is often the only mineralised part of a mollusc. The shells are usually preserved as calcium carbonate – usually any aragonite is pseudomorphed with calcite. Aragonite can be protected from recrystalization if water is kept away by carbonaceous material, but this did not accumulate in sufficient quantity until the Carboniferous; consequently aragonite older than the Carboniferous is practically unknown: but the original crystal structure can sometimes be deduced in fortunate circumstances, such as if an alga closely encrusts the surface of a shell, or if a phosphatic mould quickly forms during diagenesis.

The shell-less aplacophora have a chitinous cuticle that has been likened to the shell framework; it has been suggested that tanning of this cuticle, in conjunction with the expression of additional proteins, could have set the evolutionary stage for the secretion of a calcareous shell in an aplacophoran-like ancestral mollusc.

The molluscan shell has been internalized in a number of lineages, including the coleoid cephalopods and many gastropod lineages. Detorsion of gastropods results in an internal shell, and can be triggered by relatively minor developmental modifications such as those induced by exposure to high platinum concentrations.

Varieties

Nacre

Nacre, commonly known as mother of pearl, forms the inner layer of the shell structure in some groups of gastropod and bivalve molluscs, mostly in the more ancient families such as top snails (Trochidae), and pearl oysters (Pteriidae). Like the other calcareous layers of the shell, the nacre is created by the epithelial cells (formed by the germ layer ectoderm) of the mantle tissue.

Monoplacophora

The nacreous layer of monoplacophoran shells appears to have undergone some modification. Whilst normal nacre, and indeed part of the nacreous layer of one monoplacophoran species (*Veleropilina zografi*), consists of "brick-like" crystals of aragonite, in monoplacophora these bricks are more like layered sheets. The *c*-axis is perpendicular to the shell wall, and the *a*-axis parallel to the growth direction. This foliated aragonite is presumed to have evolved from the nacreous layer, with which it has historically been confused, but represents a novelty within the molluscs.

Chitons

The chiton *Tonicella lineata*, anterior end towards the right

Shells of chitons are made up of eight overlapping calcareous valves, surrounded by a girdle.

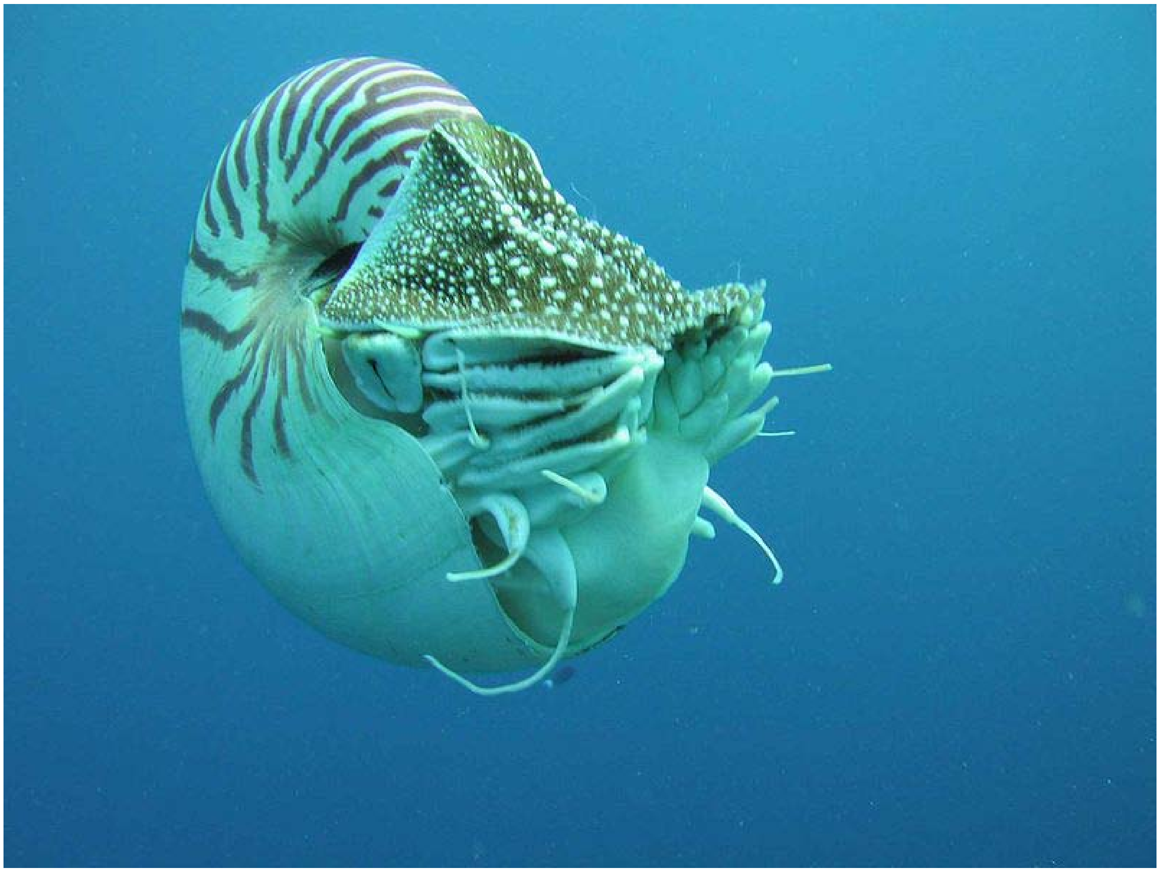
Gastropods

The marine gastropod *Cypraea chinensis*, the Chinese cowry, showing partially extended mantle

In some marine genera, during the course of normal growth the animal undergoes periodic resting stages where the shell does not increase in overall size, but a greatly thickened and strengthened lip is produced instead. When these structures are formed repeatedly with normal growth between the stages, evidence of this pattern of growth is visible on the outside of the shell, and these unusual thickened vertical areas are called *varices*, singular "varix". Varices are typical in some marine gastropod families, including the Bursidae, Muricidae, and Ranellidae.

Finally, gastropods with a determinate growth pattern may create a single and terminal lip structure when approaching maturity, after which growth ceases. These include the cowries (Cypraeidae) and helmet shells (Cassidae), both with in-turned lips, the true conchs (Strombidae) that develop flaring lips, and many land snails that develop tooth structures or constricted apertures upon reaching full size.

Cephalopods



Nautilus belauensis is one of only 6 extant cephalopod species which have an external shell

Nautiluses are the only extant cephalopods which have an external shell. Cuttlefish, squid, spirula, and cirrate octopuses have small internal shells. Females of the octopus genus *Argonauta* secrete a specialised paper-thin eggcase in which they partially reside, and this is popularly regarded as a "shell", although it is not attached to the body of the animal.

Bivalves

The shell of the Bivalvia is composed of two parts, two valves which are hinged together and joined by a ligament.

Scaphopods

Tusk shell of *Antalis vulgaris*.

The shell of many of the scaphopods ("tusk shells") resembles a miniature elephant's tusk in overall shape, except that it is hollow, and is open at both ends.

Damage to shells in collections

As a structure made primarily of calcium carbonate, mollusc shells are vulnerable to attack by acidic fumes. This can become a problem when shells are in storage or on display and are in the proximity of non-archival materials.

Chapter- 6

Water Vascular System

The **water vascular system** is a hydraulic system used by echinoderms, such as sea stars and sea urchins, for locomotion, food and waste transportation, and respiration. The system is composed of canals connecting numerous tube feet. Echinoderms move by alternately contracting muscles that force water into the tube feet, causing them to extend and push against the ground, then relaxing to allow the feet to retract..

The exact structure of the system varies somewhat between the five classes of echinoderm.

Sea stars

In sea stars (starfish), water enters the system through a sieve-like structure on the upper surface of the animal, called the madreporite. This overlies a small sac, or ampulla connected to a duct termed the stone canal, which is, as its name implies, commonly lined with calcareous material. The stone canal runs to a circular ring canal, from which radial canals run outwards along the ambulacral grooves. Each arm of a sea star has one such groove on its underside, while, in sea urchins, they run along the outside of the body.

Each side of the radial canals gives rise to a row of bulb-like ampullae. These are always staggered, so that an ampulla on the left follows one on the right, and so on down the length of the radial canal. The ampullae are connected to suckerlike podia, the entire structure is called a tube foot. In most cases, the small lateral canals connecting the ampullae to the radial canal are of equal length, so that the tube feet are arranged in two rows, one along each side of the groove. In some species, however, there are alternately long and short lateral canals, giving the appearance of two rows on each side of the groove, for four in total.

Contraction of the ampullae causes the podia to stretch as water is brought into them. This whole process allows for movement, and is quite powerful but extremely slow.

The central ring canal, in addition to connecting the radial canals to each other and to the stone canal, also has a number of other specialised structures on the inner surface. In between each radial canal, in many sea star species, there lies a muscular sac called a polian vesicle. The radial canal also has four or five pairs of complex pouches, called Tiedemann's bodies. These apparently produce coelomocytes, amoeboid cells somewhat similar to the blood cells of vertebrates.

Although the contents of the water vascular system are essentially sea water, apart from coelomocytes, the fluid also contains some protein and high levels of potassium salts.

Ophiuroids

Ophiuroids, the group including brittle stars and basket stars, have a somewhat different water vascular system from sea stars, despite their superficially similar appearance. The madreporite is located on the underside of the animal, usually in one of the jaw plates. The stone canal runs upwards to the ring canal, typically located in a circular depression on the upper (i.e. internal) surface of the jaws. The ring canal has four polian vesicles.

Ophiuroids have no ambulacral groove, and the radial canals instead run through the solid bone-like ossicles of the arms. Unlike sea stars, the tube feet are paired instead of staggered, and there are no ampullae. Instead, a simple valve at the upper end of the foot helps to control water pressure in the tube feet, along with contraction of the associated canals.

Sea urchins

The madreporite of sea urchins is located within one of the plates surrounding the anus on the upper surface of the animal. The stone canal descends from the madreporite to the ring canal, which lies around the oesophagus, and includes a number of polian vesicles. Because sea urchins have no arms, the five radial canals simply run along the inside of the solid skeletal "test", arching upwards towards the anus.

The ampullae branching off from either side of the radial canals give rise to ten rows of tube feet, which penetrate through holes in the test to the outside. As in sea stars, the ampullae are arranged alternately, but in most (though not all) cases they split into two as they pass through the test before merging again on the outer side. The tube feet of sea urchins are often highly modified for different purposes. The radial canal ends in a small water-filled tentacle which protrudes through the uppermost plate of the ambulacral region.

Crinoids

Uniquely among echinoderms, crinoids have no madeporite. Instead, the oral surface is dotted within numerous minute ciliated funnels that run into the main body cavity. The ring canal has several small stone canals, located between the arms of the animal, but these open into the body cavity, and thus are only indirectly connected to the outside.

The five radial canals run into the arms and branch several times to supply all of the individual branches and pinnules lining the arms. As in other echinoderms, the radial canals give rise to lateral canals, but there are no ampullae, and clusters of three tube feet branch from the ends of each canal, except around the mouth, where they are found singly. In the absence of ampullae, water pressure is maintained by the ring canal, which is surrounded by contractile muscle fibres.

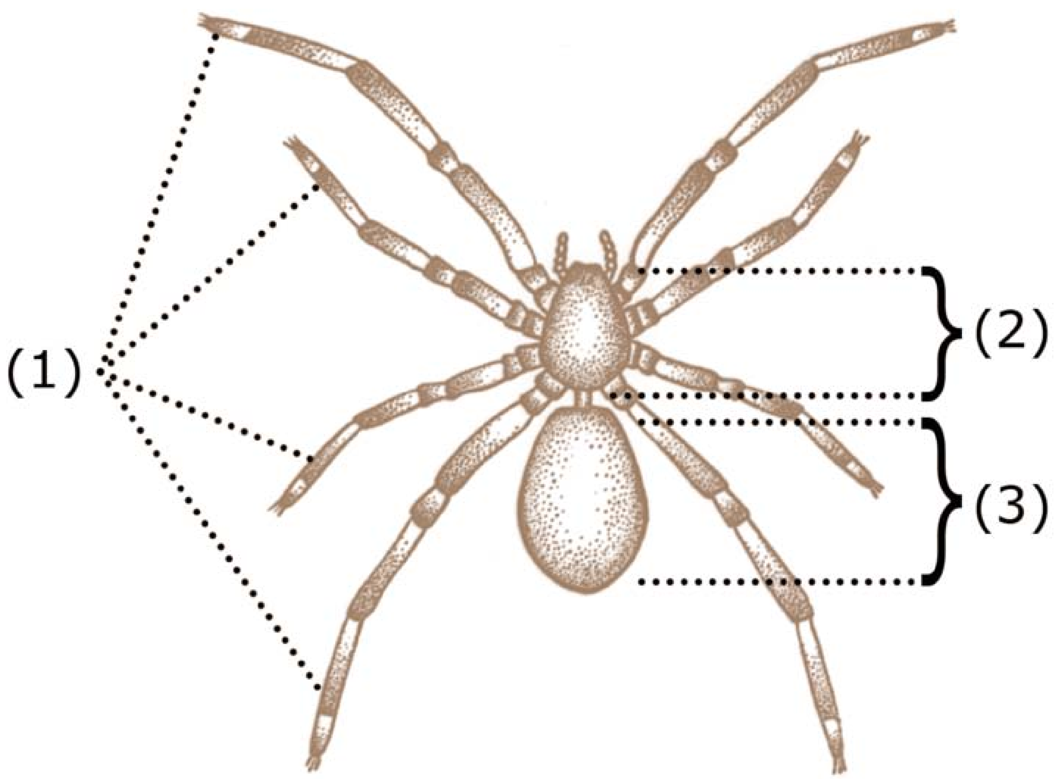
Sea cucumbers

The water vascular system of sea cucumbers has no connection to the outside, and is thus filled with the internal coelomic fluid, rather than sea water. The madreporite is present, but lies within the body cavity, just below the pharynx. The stone canal is relatively short.

The ring canal normally has one to four polian vesicles, but in the order Apodida, there may be as many as fifty. The radial canals run through notches in the calcareous plates surrounding the mouth and then run along the ambulacral areas along the length of the body. Lateral canals run to both the tube feet and the large oral tentacles, all of which possess ampullae. The Apodida, which have no tube feet, also have no radial canals, with the canals to the tentacles branching off directly from the ring canal.

Chapter- 7

Spider Anatomy

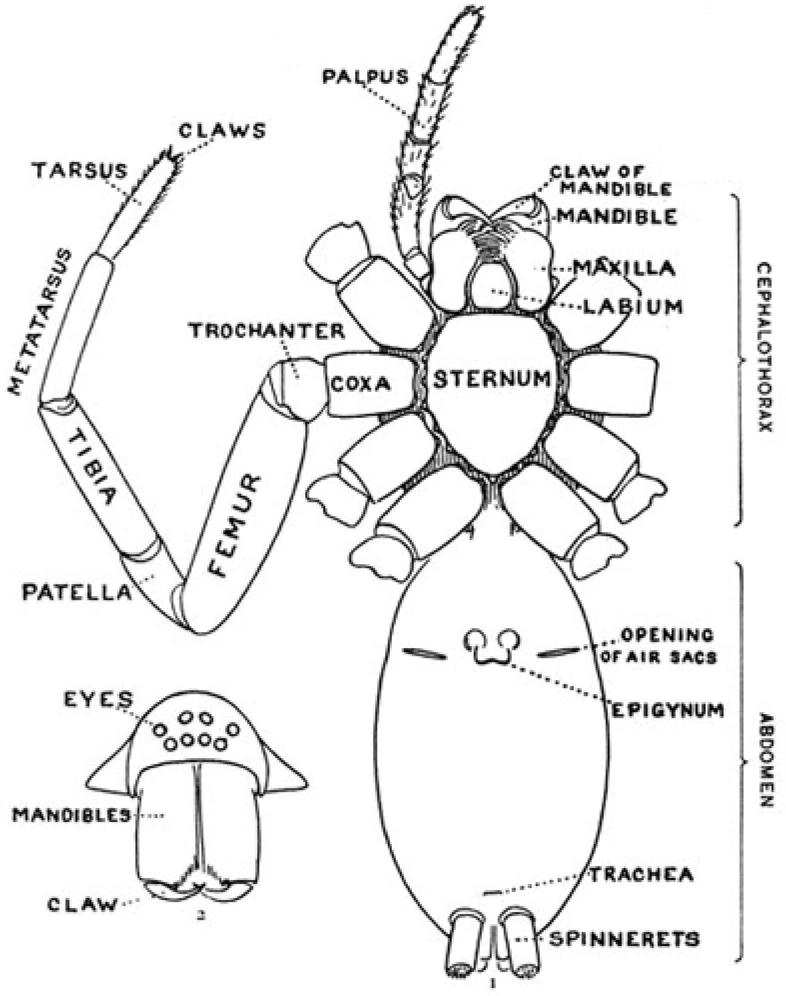


Basic characteristics of arachnids include four pairs of legs (1) and a body divided into two segments: the cephalothorax (2) and the abdomen (3).

The **anatomy** of **spiders** includes many characteristics shared with other arachnids. These characteristics include bodies divided into two segments, eight jointed legs, no wings or antennae, the presence of chelicerae and pedipalps, simple eyes, and an exoskeleton which is periodically shed.

Spiders also have several adaptations that distinguish them from other arachnids. All spiders are capable of producing silk of various types, which many species use to build webs to ensnare prey. Most spiders possess venom which is injected into prey (or defensively, when the spider feels threatened) through the fangs of the chelicerae. Male spiders have specialized pedipalps which are used to transfer sperm to the female during mating. Many species of spiders exhibit a great deal of sexual dimorphism.

External anatomy



The underside and head of a spider

The ventral side of a Brown Widow spider. The epigastric plates and furrow are visible, as well as the hourglass marking on the underside of the abdomen which is a characteristic feature of widow spiders.

Spiders, unlike insects, have only two tagmata instead of three: a fused head and thorax (called a cephalothorax or prosoma) and an abdomen (called the opisthosoma). The exception to this rule are the assassin spiders, whose cephalothorax is divided into two parts by an elongated "neck". Except for a few species of very primitive spiders (family *Liphistiidae*, also called *segmented spiders*), the abdomen is not externally segmented. The abdomen and cephalothorax are connected with a thin waist called the pedicle or the *pregenital somite*, a trait that allows the spider to move the abdomen in all directions. This waist is actually the last segment (somite) of the cephalothorax and is lost in most other members of the Arachnida (in scorpions it is only detectable in the embryos). Unlike insects, spiders have an endoskeleton in addition to their exoskeleton.

Cephalothorax

Most external appendages on the spider are attached to the cephalothorax, including the legs, eyes, chelicerae and other mouthparts, and pedipalps.

Spiders typically have eight legs (insects have six), no antennae, and their eyes are single lenses rather than compound eyes. They have pedipalps (or just *palps*), at the base of which are coxae or maxillae next to their mouth that aid in ingesting food; the ends of the palp are modified in adult males into elaborate and often species-specific structures used for mating. Since they don't have any antennae, they are using specialised and sensitive hairs on their legs to pick up scent, sounds, vibrations and air currents.

Like other Arachnids, spiders are unable to chew their food, so they have a mouth part shaped like a short drinking straw which they use to suck up the liquified insides of their prey. However, they are able to eat their own silk to recycle proteins needed in the production of new spider webs. Some spiders, such as the dewdrop spiders *(Argyrodes)*, even eat the silk of other spider species.

Eyes, vision, and sense organs

Multiple eyes of a jumping spider

Spiders usually have eight eyes in various arrangements, a fact which is used to aid in taxonomically classifying different species. Most species of the Haplogynae have six eyes, although some have eight (Plectreuridae), four (e.g., Tetrablemma) or even two (most Caponiidae) eyes. Sometimes one pair of eyes is better developed than the rest, or even, in some cave species, there are no eyes at all. Several families of hunting spiders, such as jumping spiders and wolf spiders, have fair to excellent vision. The main pair of eyes in jumping spiders even sees in colors.

Net-casting spiders have enormous, compound lenses that give a wide field of view and gather available light very efficiently. The lenses have an F number of 0.58 which means they can concentrate available light more efficiently than a cat (F 0.9) or an owl (F 1.1). Each night a large area of light sensitive membrane is manufactured within these eyes (and rapidly destroyed again at dawn).

However, most spiders that lurk on flowers, webs, and other fixed locations waiting for prey tend to have very poor eyesight; instead they possess an extreme sensitivity to vibrations, which aids in prey capture. Vibration sensitive spiders can sense vibrations from such various mediums as the water surface, the soil or their silk threads. Also changes in the air pressure can be detected in the search for prey.

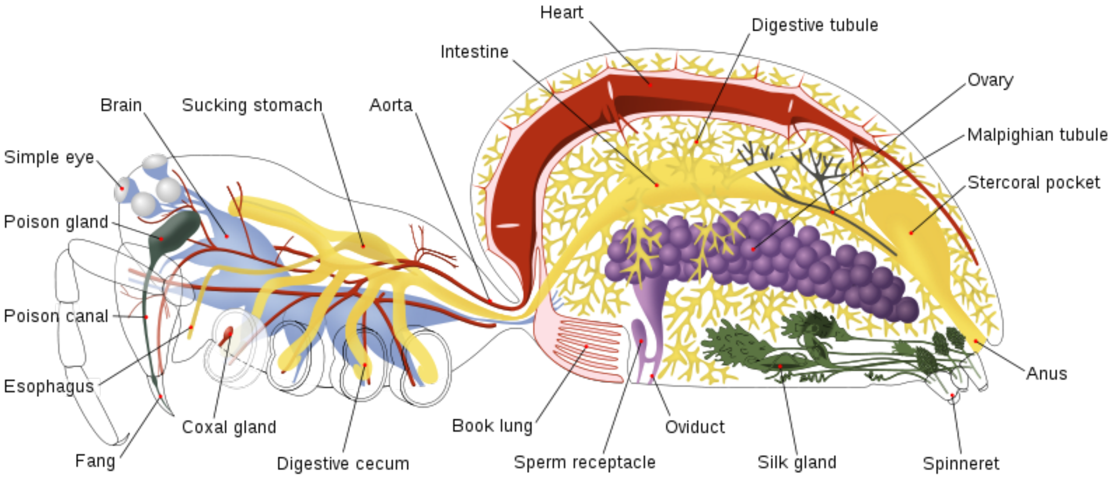
Abdomen

On the ventral side of the abdomen are two hardened plates which cover the book lungs. These are called the **epigastric plates**. A fold, known as the **epigastric furrow**, separates the region of the book lungs and epigyne from the more posterior part of the abdomen. In the middle of this furrow is the opening of the oviduct (in females) and at either end are the lung slits.

Spinnerets

The abdomen has no appendages except from one to four (usually three) modified pairs of movable telescoping organs called spinnerets, which produce silk. Originally, the common ancestor of spiders had four pairs of spinnerets, with two pairs on the tenth body segment and two pairs on the eleventh body segment, located in the middle on the ventral side of the abdomen. The suborder *Mesothelae* is unique in having only two types of silk glands - thought to be the ancestral condition. All other spiders have the spinnerets further towards the posterior end of the body where they form a small cluster, and the anterior central spinnerets on the tenth segment are lost or reduced (suborder *Mygalomorphae*), or modified into a specialised and flattened plate called the cribellum (suborder *Araneomorphae*). The cribellum (usually separated into a left and a right half) produces a thread which is made up of hundreds to thousands of very fine dry silk fibers (about 10 nm thick) around a few thicker core fibers, which then are combed into a woolly structure by using a group of specialized hairs (setae) on their fourth pair of legs. It is suspected their woolly silk is charged with static electricity, causing its fine fibres to attach to trapped prey. Once all araneomorph (modern) spiders had a cribellum, but today it only remains in the cribellate spiders (although it is sometimes missing even here), which are widespread around the world. Often, this plate lacks the ability to produce silk, and is then called the **colulus**; an organ which zoologists have not identified a function for. The colulus is reduced or absent in most species. The cribellate spiders were the first spiders to build specialised prey catching webs, later evolving into groups which used the spinnerets solely to make webs, instead using silk threads dotted with droplets of a sticky liquid (like pearls on a necklace) to capture small arthropods, and a few large species even small bats and birds. Other spiders don't build webs at all, but have become active hunters, like the highly successful jumping spiders.

Internal anatomy

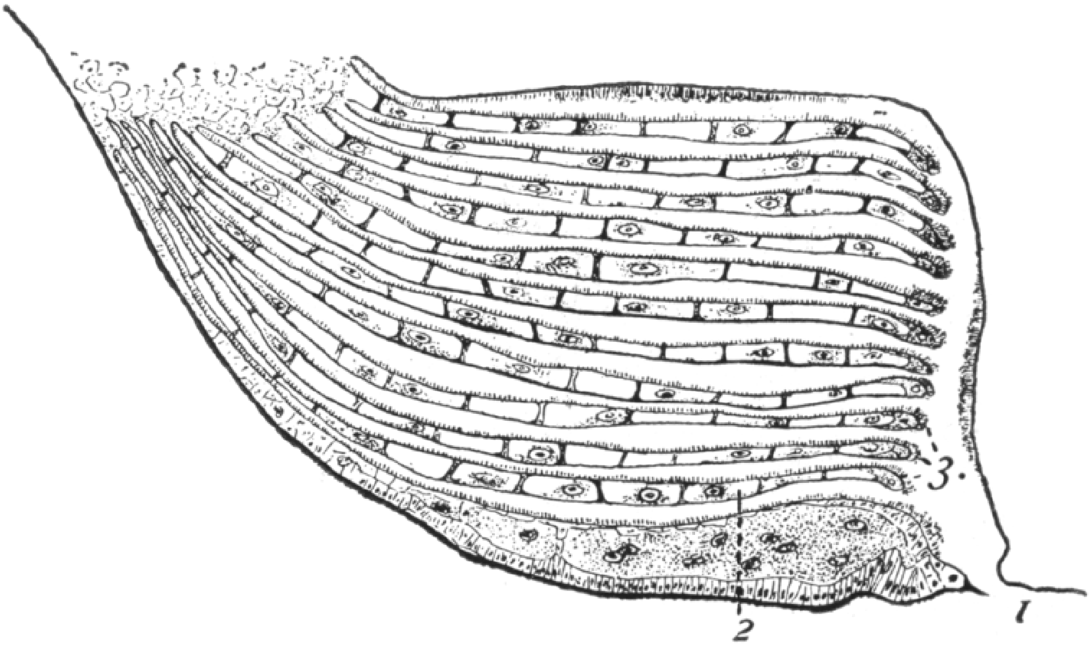


Circulation

Spiders, like most arthropods, have an open circulatory system, i.e., they do not have true blood, or veins to convey it. Rather, their bodies are filled with haemolymph, which is pumped through arteries by a heart into spaces called sinuses surrounding their internal organs. The haemolymph contains hemocyanin, a respiratory protein similar in function to hemoglobin. Hemocyanin contains two copper atoms, tinting the haemolymph with a faint blue color.

The heart is located in the abdomen a short distance within the middle line of the dorsal body-wall, and above the intestine. Unlike in insects, the heart is not divided into chambers, but consists of a simple tube. The aorta, which supplies haemolymph to the cephalothorax, extends from the anterior end of the heart. Smaller arteries extend from sides and posterior end of the heart. A thin-walled sac, known as the pericardium, completely surrounds the heart.

Breathing



Spider book lungs (cross section)

Spiders have developed several different respiratory anatomies, based either 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. This system has most likely evolved in small ancestors to help resist desiccation. The trachea were originally connected to the surroundings through a pair of spiracles, but in the majority of spiders this pair of spiracles has fused into a single one in the middle, and migrated posterior close to the spinnerets.

Among smaller araneomorph spiders we can find species who have evolved also the anterior pair of book lungs into trachea, or the remaining book lungs are simply reduced or missing, and in a very few the book lungs have developed deep channels, apparently signs of evolution into tracheae. Some very small spiders in moist and sheltered habitats don't have any breathing organs at all, as they are breathing directly through their body surface. In the tracheal system oxygen interchange is much more efficient, enabling cursorial hunting (hunting involving extended pursuit) and other advanced characteristics as having a smaller heart and the ability to live in drier habitats.

Digestion

Spider feeding on silk-wrapped grasshoper

Digestion is carried out internally and externally. Spiders that do not have powerful chelicerae secrete digestive fluids into their prey from a series of ducts perforating their chelicerae. The coxal glands are excretory organs that lie in the prosoma, and open to the outside at the coxae of the walking legs. In primitive spiders, such as the Mesothelae and the Orthognata, two pairs of coxal glands open onto the posterior side of the first and third coxae. They release a fluid only during feeding and play an important role in ion and water balance. Digestive fluids dissolve the prey's internal tissues. Then the spider feeds by sucking the partially digested fluids out. Other spiders with more powerfully built chelicerae masticate the entire body of their prey and leave behind only a relatively small glob of indigestible materials. Spiders consume only liquid foods. Many spiders will store prey temporarily. Web weaving spiders that have made a shroud of silk to quiet their envenomed prey's death struggles will generally leave them in these shrouds and then consume them at their leisure.

Reproductive system

Almost all spiders reproduce sexually. They are unusual in that they do not transfer sperm directly, for example via a penis. Instead the males transfer it to specialized pedipalps and then meander about to search for a mate. These palps are then introduced into the female's epigyne. This was first described in 1678 by Martin Lister. In 1843 it was revealed that males build a nuptial web into which they deposit a drop of semen, which is then taken up by the copulatory apparatus in the pedipalp. The structure of the copulatory apparatus varies significantly between males of different species. While the widened palpal tarsus of *Filistata hibernalis* (Filistatidae) only forms a kind of bulb containing the coiled blind duct, members of the genus *Argiope* have a highly complex structure.

Glossary

Spider anatomy acronyms

acronym	meaning
ALE	anterior lateral eyes
AME	anterior median eyes
DTA	dorsal tegular apophysis
DTiA	dorsal tibial apophysis
LTA	lateral tegular apophysis
MOQ	median ocular quadrangle
PLE	posterior lateral eyes

PLS	posterior lateral spinnerets
PME	posterior median eyes
PMS	posterior median spinnerets
RCF	retrolateral cymbial fold
RTA	retrolateral tibial apophysis
VTA	ventral tegular apophysis
VTiA	ventral tibial apophysis

Chapter- 8

Evolution of Spiders

A spider in Baltic amber

The **evolution of spiders** has been going on for at least 400 million years, since the first true spiders (thin-waisted arachnids) evolved from crab-like chelicerate ancestors. Today, there are over 40,000 described spider species within the diverse phylum of arthropods.

Major developments in spider evolution include the development of spinnerets and silk secretion, as well as different adaptions for its use.

Early spider-like arachnids

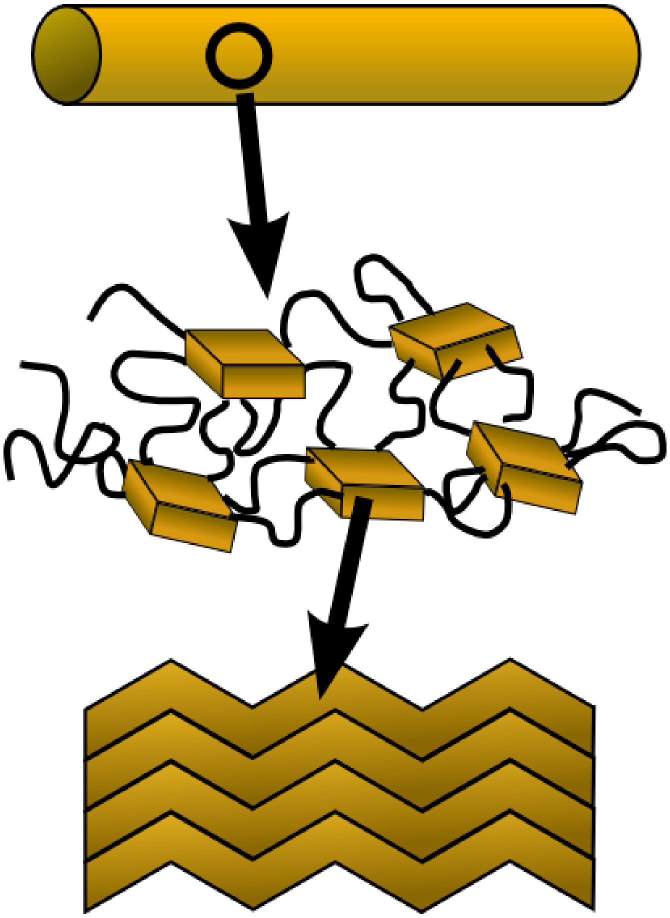
Among the oldest known land arthropods are Trigonotarbids, members an extinct order of spider-like arachnids.

Sharing many superficial characteristics with spiders, Trigonotarbida were terrestrial, respired through book lungs, and walked on eight legs with two additional legs adapted to use around their mouth. Arguments still remain open as to whether they possessed the ability to create silk. This had been popular thought for quite some time, until an unpublished fossil was described with distinct microtubercles on its hind legs, akin to those used by spiders to direct and manipulate their silk.

Regardless Trigonotarbida are not considered true-spiders. They are generally accepted as an independent early offshoot within the Arachnida clade, and not directly ancestral to modern spiders.

Emergence of true spiders

At one stage the oldest fossil spider was believed to be *Attercopus* which lived 380 million years ago during the Devonian. *Attercopus* was placed as the sister-taxon to all living spiders, but has now been reinterpreted as a member of a separate, extinct order Uraraneida which could produce silk, but did not have true spinnerets.



Microscopic structure of spider silk, possibly the most important adaption developed during the evolution of these arachnids

The oldest true spiders are thus Carboniferous in age, or about 300 million years. Most of these early segmented fossil spiders from the Coal Measures of Europe and North America probably belonged to the Mesothelae, or something very similar, a group of primitive spiders with the spinnerets placed underneath the middle of the abdomen, rather than at the end as in modern spiders. They were probably ground dwelling predators, living in the giant clubmoss and fern forests of the mid-late Palaeozoic, where they were presumably predators of other primitive arthropods. Silk may have been used simply as a protective covering for the eggs, a lining for a retreat hole, and later perhaps for simple ground sheet web and trapdoor construction.

As plant and insect life diversified so also did the spider's use of silk. Spiders with spinnerets at the end of the abdomen (Mygalomorphae and Araneomorphae) appeared more than 250 million years ago, presumably promoting the development of more elaborate sheet and maze webs for prey capture both on ground and foliage, as well as the development of the safety dragline. The oldest mygalomorph, Rosamygale, was described from the Triassic of France and belongs to the modern family Hexathelidae. Megarachne servinei from the Permo-Carboniferous was once thought to be a giant mygalomorph spider and, with its body length of 1 foot (34 cm) and leg span of above 20 inches (50 cm), the largest known spider ever to have lived on Earth, but subsequent examination by an expert revealed that it was actually a middling-sized sea scorpion.

By the Jurassic, the sophisticated aerial webs of the orb-weaver spiders had already developed to take advantage of the rapidly diversifying groups of insects. A spider web preserved in amber, thought to be 110 million years old, shows evidence of a perfect "orb" web, the most famous, circular kind one thinks of when imagining spider webs. An examination of the drift of those genes thought to be used to produce the web-spinning behavior suggests that orb spinning was in an advanced state as many as 136 million years ago.

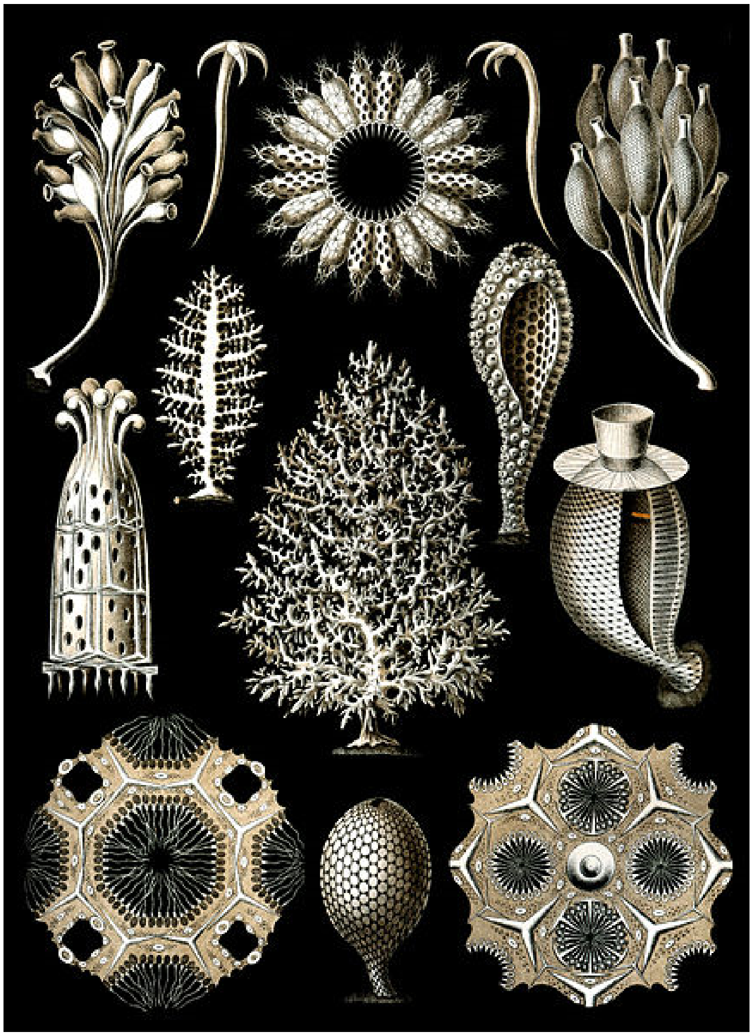
The 110-million-year-old amber-preserved web is also the oldest to show trapped insects, containing a beetle, a mite, a wasp's leg, and a fly. The ability to weave orb webs is thought to have been "lost", and sometimes even re-evolved or evolved separately, in different breeds of spiders since its first appearance.

Chapter- 9

Different Classes of Sponges

1. Calcareous sponge

Calcareous sponges



"Calcispongiae" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification

Kingdom:	Animalia
Phylum:	Porifera
Class:	**Calcarea** Bowerbank, 1817

Subclasses

Calcinea
Calcaronea

The **calcareous sponges** of class **Calcarea** are members of the animal phylum Porifera, the cellular sponges. They are characterized by spicules made out of calcium carbonate in the form of calcite or aragonite. While the spicules in most species have three points, in some species they have either two or four points.

Biology

Clathrina clathrus, an asconoid calcareous sponge

All sponges in this class are strictly marine, and, while they are distributed worldwide, most are found in shallow tropical waters. Like all other sponges, they are sedentary filter feeders.

All three sponge body plans are represented within class Calcarea : asconoid, syconoid, and leuconoid. Typically, calcareous sponges are small, measuring less than 10 centimetres (3.9 in) in height, and drab in colour. However, a few brightly coloured species are also known.

Calcareous sponges vary from radially symmetrical vase-shaped body types to colonies made up of a meshwork of thin tubes, or irregular massive forms. The skeleton has either a mesh or honeycomb structure.

Classification

Of the 15,000 or so species of Porifera that exist, only 400 of those are Calcareans.

Calcarean sponges first appeared during the Cambrian and their diversity was greatest during the Cretaceous period. Recent molecular analysis suggests that the class Calcarea should be designated as a phylum, in particular the first to have diverged in the Kingdom Animalia; the other sponges belong to the phylum Silicarea.

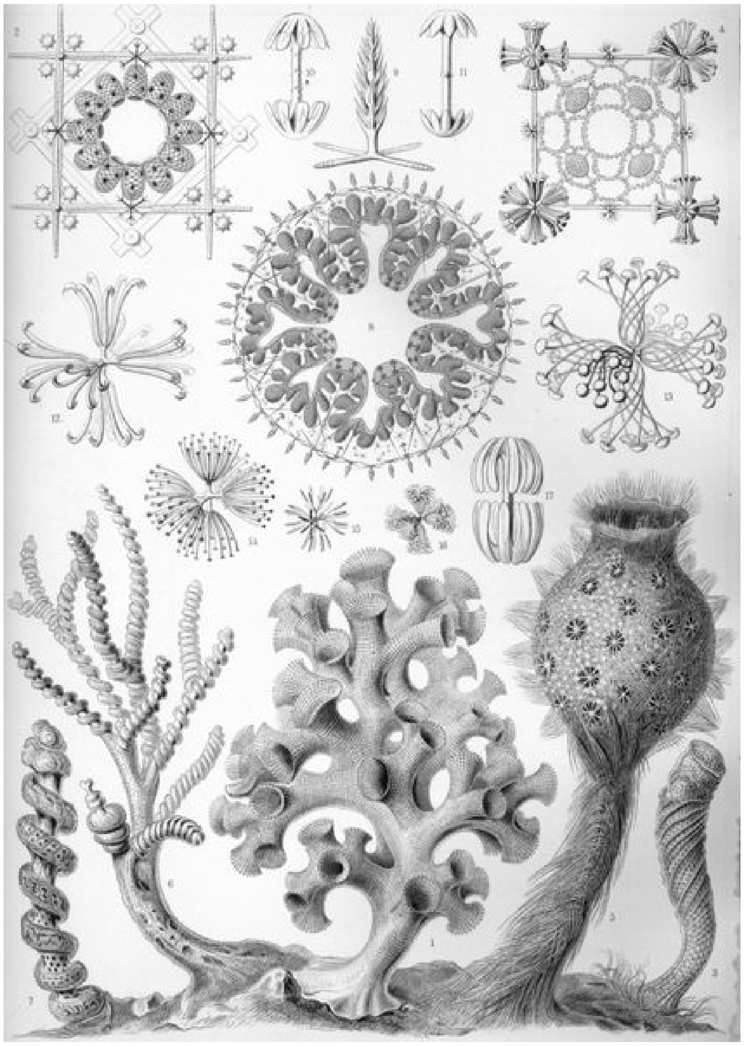
The calcareous sponges are divided into two subclasses and seven orders:

Class **Calcarea**

- Subclass Calcinea
    - Order Clathrinida
    - Order Leucettida
    - Order Murrayonida
- Subclass Calcaronea
    - Order Baerida
    - Order Leucosolenida
    - Order Lithonida
    - Order Sycettida

2. Hexactinellid

Hexactinellid sponges
Temporal range: Cambrian–Recent



"Hexactinellae" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification

Kingdom:	Animalia
Phylum:	Porifera
Class:	**Hexactinellida** Schmidt, 1870

Subclasses

- Amphidiscophora
- Hexasterophora

Hexactinellid sponges are sponges with a skeleton made of four- and/or six-pointed silaceous spicules, often referred to as **glass sponges**. They are usually classified along with other sponges in the phylum Porifera, but some researchers consider them sufficiently distinct to deserve their own phylum, **Symplasma**.

Biology

Staurocalyptus sp.

Glass sponges are relatively uncommon and are mostly found at depths from 450 to 900 metres (1,480 to 3,000 ft) although the species *Oopsacas minuta* has been found in shallow water, while others have been found much deeper. They are found in all oceans of the world, although they are particularly common in Antarctic waters.

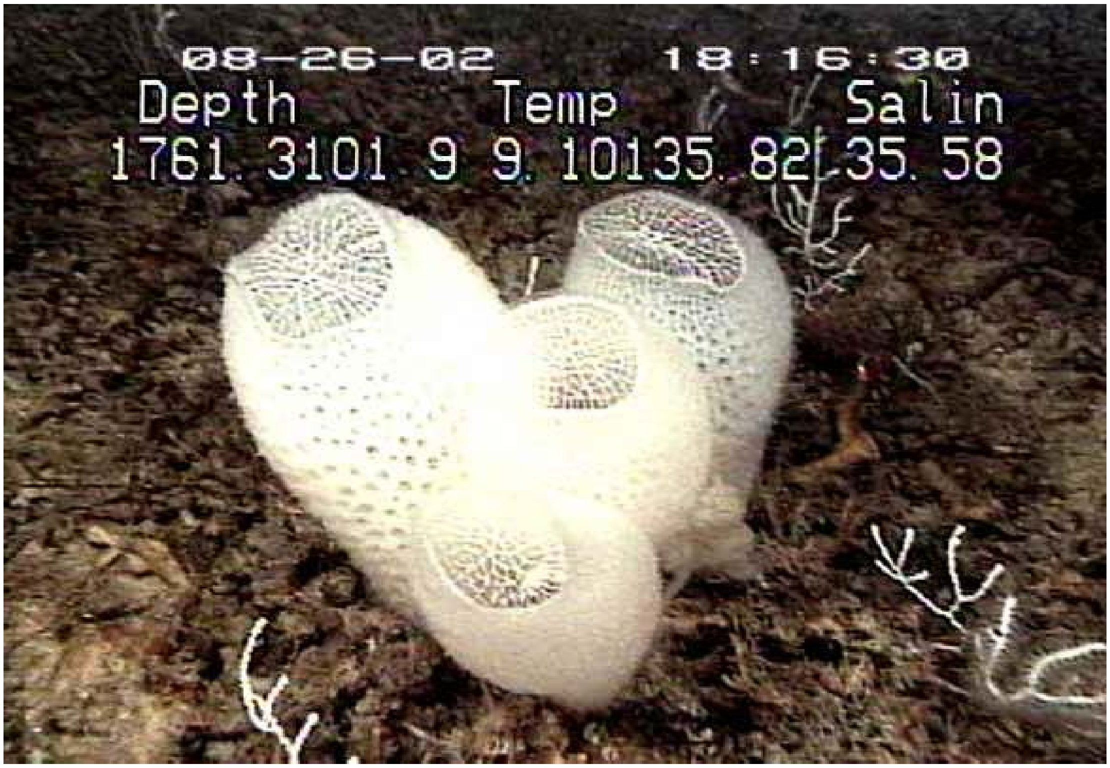
They are more-or-less cup-shaped animals, ranging from 10 to 30 centimetres (3.9 to 12 in) in height, with sturdy lattice-like internal skeletons made up of fused spicules of silica. The body is relatively symmetrical, with a large central cavity that, in many species, opens to the outside through a sieve formed from the skeleton. Unlike other sponges, they tend to be present as individuals, rather than forming large fused colonies. They are generally pale in colour.

Much of the body is composed of syncitia, extensive regions of multinucleate cytoplasm. In particular, the epidermal cells of other sponges are absent, being replaced by a syncitial net of amoebocytes, through which the spicules penetrate. Unlike other sponges, they do not possess the ability to contract.

One ability they possess is a unique system for rapidly conducting electrical impulses across their bodies, making it possible for them to respond quickly to external stimuli. Glass sponges like "Venus' Flower Basket" have a tuft of fibers that extends outward like an inverted crown at the base of their skeleton. These fibers are 50 to 175 millimetres (2.0 to 6.9 in) long and about the thickness of a human hair. They work as optical fibers somewhat similar to those used in modern telecommunication networks.

Glass sponges are different from other sponges in a variety of other ways. For example, most of the cytoplasm is not divided into separate cells by walls but forms a syncytium or continuous

mass of cytoplasm with many nuclei (e.g., Reiswig and Mackie, 1983).



Venus' Flower Basket, *Euplectella aspergillum*

These creatures live for a very long time, but the exact age is hard to measure; one study based on modelling gave an estimated age of a specimen of *Scolymastra joubini* as 23,000 years, which is thought impossible, but is the basis for a listing of ~15,000 years in the AnAge Database. The shallow water occurrence of hexactinellids is rare world wide. In the Antarctic two species occur as shallow as 33 meters under the ice. In the Mediterranean one species occurs as shallow as 18 meters in a cave with deep water upwelling (Boury-Esnault & Vacelet (1994)

Reefs

The sponges form reefs off the coast of British Columbia and Washington State, which are studied in the Sponge Reef Project.

Classification

The earliest known hexactinellids are from the earliest Cambrian or late Neoproterozoic. They are fairly common relative to demosponges as fossils, but this is thought to be, at least in part, because their spicules are sturdier than spongin and fossilize better. Like almost all sponges, the hexactinellids draw water in through a series of small pores by the whip like beating of a series of hairs or flagella in chambers which in this group line the sponge wall. (Sponge Gardens)

The class is divided into six orders, in two subclasses:

Class **Hexactinellida**

- Subclass Amphidiscophora
    - Order Amphidiscosida
- Subclass Hexasterophora
    - Order Aulocalycoida
    - Order Hexactinosa
    - Order Lychniscosa
    - Order Lyssacinosa

3. Demosponge

Demospongiae

Barrel sponge (*Xestospongia testudinaria*)

Scientific classification

Kingdom:	Animalia
Phylum:	Porifera
Class:	**Demospongiae** Sollas, 1885

Subclasses

Homoscleromorpha
Tetractinomorpha
Ceractinomorpha

The **Demospongiae** are the largest class in the phylum Porifera. Their "skeletons" are made of spicules consisting of fibers of the protein spongin, the mineral silica, or both. Where spicules of silica are present, they have a different shape from those in the otherwise similar glass sponges. The demosponges include 90% of all species of sponges and are predominantly leuconoid in structure.

There are many diverse orders in this class, including all of the large sponges. Most are marine dwellers, but several live in freshwater environments. Some species are brightly colored, and there is great variety in body shape; the largest species are over 1 metre (3.3 ft) across. They reproduce both sexually and asexually.

Classification

The Demospongia have an ancient history with the first demosponge fossils appearing in Precambrian deposits at the end of the Cryogenian "Snowball Earth" period, where their presence has been detected by fossilized steroids, called steranes, hydrocarbon markers that are characteristic of the cell membranes of the sponges, rather than from direct fossils of the sponges themselves. They represent a continuous 100-Myr-long chemical fossil record of demosponges through the end of the Neoproterozoic. The earliest sponge-bearing reefs date to the Early Cambrian, exemplified by a small bioherm constructed by archaeocyathids and calcified microbes at the start of the Tommotian stage (about 540–535 Ma), found in southeast Siberia. A major radiation occurred in the Lower Cambrian and further major radiations in the Ordovician possibly from the middle Cambrian. (Finks, 1970

The extant Demospongiae have been organised into 14 orders that encompass 88 families, 500 genera and more than 8000 described species.

Hooper and van Soest give the following classification of demosponges into orders:

- Subclass **Homoscleromorpha** Bergquist 1978
  - Homosclerophorida Dendy 1905
- Subclass **Tetractinomorpha**
  - Astrophorida Sollas 1888
  - Chondrosida Boury-Esnault & Lopès 1985
  - Hadromerida Topsent 1894
  - Lithistida Sollas 1888
  - Spirophorida Bergquist & Hogg 1969
- Subclass **Ceractinomorpha** Levi 1953
  - Agelasida Verrill 1907
  - Dendroceratida Minchin 1900
  - Dictyoceratida Minchin 1900
  - Halichondrida Gray 1867
  - Halisarcida Bergquist 1996
  - Haplosclerida Topsent 1928
  - Poecilosclerida Topsent 1928
  - Verongida Bergquist 1978
  - Verticillitida Termier & Termier 1977

However, molecular evidence suggests that the *Homoscleromorpha* may not belong in this class and that other classifications may need to be revised.

Systematics

Monanchora barbadensis (red encrusting sponge)

Demosponge systematics is an active area of research, and much is still to be learned. However, some rudimentary outlines can be made. The basal clade of the Demospongia is the Homoscleromorpha, characterized by the possession of a larva more reminiscent of that of the Calcarea than that of the rest of the Demospongia. Demosponges other than the Homoscleromorpha are split into two major groups, the Tetractinomorpha and the Ceractinomorpha. These two groups share characters that indicate common descent such as a distinctive larval type and the presence of spongin. Currently, the two groups are each characterized by distinctive types of microscleres, though some doubt still remains as to whether the distinctive microsclere types evolved only once in each group. Fossils of each of these groups is known from the Cambrian suggesting an early radiation of the major clades of demosponges. The Lithistida, a taxonomic grouping into which many of the fossil demosponges fall, is most certainly polyphyletic with members in both the Tetractinomorpha and the Ceractinomorpha.

A molecular study of the mitochondrial genome suggests that five major clades exist in the Demospongiae. These clades are

- Homoscleromorpha: order Homosclerophorida

- Keratosa: orders Dendroceratida, Dictyoceratida and Verticillitida
- Myxospongiae: orders Chondrosida, Halisarcida and Verongida
- Haplosclerida (marine species)
- Remainder of the demosponges: orders Agelasida, Astrophorida, Hadromerida, Halichondrida, Poecilosclerida, Spirophorida and Haploscerida (freshwater species)

The branching order appears to be (Homoscleromorpha, (Keratosa, Myxospongiae)(Haplosclerida [marine species], Remainder of the demosponges))

Reproduction

Red volcano sponge (*Acarnus erithacus*).

Spermatocytes develop from the transformation of choanocytes and oocytes arise from archeocytes. Repeated cleavage of the zygote egg takes place in the mesohyl and forms a parenchymula larva with a mass of larger internal cells surrounded by small, externally flagellated cells. The resulting swimming larva enters a canal of the central cavity and is expelled with the exhalant current.

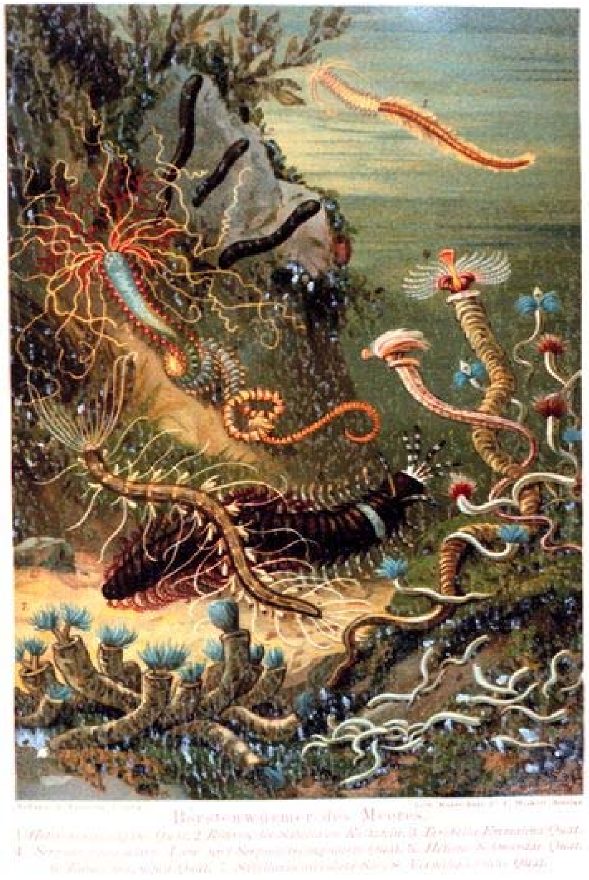
Methods of asexual reproduction include both budding and the formation of gemmules. In budding, aggregates of cells differentiate into small sponges that are released superficially or expelled through the oscula. Gemmules are found in the freshwater family Spongellidae. They are produced in the mesohyl as clumps of archeocytes, are surrounded with a hard layer secreted by other amoebocytes. Gemmules are released when the parent body breaks down, and are capable of surviving harsh conditions. In a favorable situation, an opening called the micropyle appears and releases amoebocytes, which differentiate into cells of all the other types.

Chapter- 10

Classification and Diversity of Annelids

1. Polychaete

Polychaetes
Fossil range: 530–0 Ma
Cambrian (or earlier?) - present



"A variety of marine worms": plate from *Das Meer* by M. J. Schleiden (1804–1881).

Scientific classification	
Kingdom:	Animalia
Phylum:	Annelida
Class:	**Polychaeta** Grube, 1850
Subclasses	
Palpata Scolecida	

The **Polychaeta** or **polychaetes** are a class of annelid worms, generally marine. Each body segment has a pair of fleshy protrusions called parapodia that bear many bristles, called chaetae, which are made of chitin. Indeed, polychaetes are sometimes referred to as **bristle worms**. More than 10,000 species are described in this class. Common representatives include the lugworm (*Arenicola marina*) and the sandworm or clam worm *Nereis*.

Polychaetes as a class are robust and widespread, with species that live in the coldest ocean temperatures of the abyssal plain, to forms which tolerate the extreme high temperatures near hydrothermal vents. Polychaetes occur throughout the Earth's oceans at all depths, from forms that live as plankton near the surface, to a 2–3 cm specimen (still unclassified) observed by the robot ocean probe Nereus at the bottom of the Challenger Deep, the deepest spot in the Earth's oceans.

Description

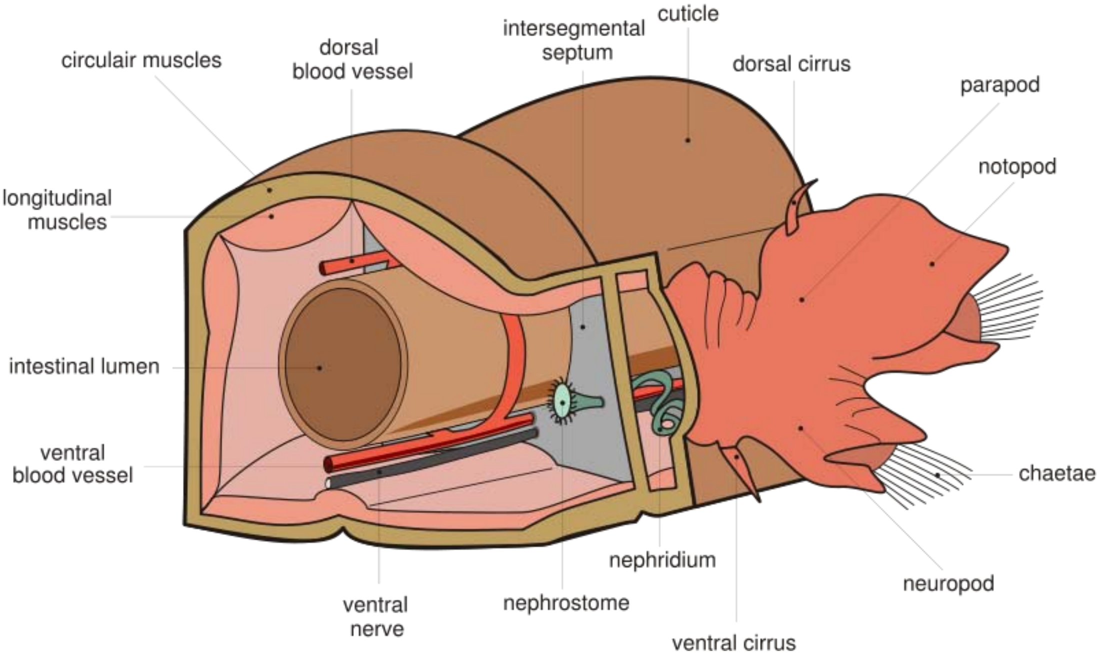
Polychaetes are segmented worms, generally less than 10 centimetres (3.9 in) in length, although ranging at the extremes from 1 millimetre (0.039 in) to 3 metres (9.8 ft). They are often brightly coloured, and may be iridescent or even luminescent. Each segment bears a pair of paddle-like and highly vascularized parapodia, which are used for movement and, in many species, act as the worm's primary respiratory surfaces. Bundles of bristles, called setae, project from the parapodia.

However, polychaetes vary widely from this generalised pattern, and can display a range of different body forms. The most generalised polychaetes are those that crawl along the bottom, but others have adapted to many different ecological niches, including burrowing, pelagic life, tube-dwelling or boring, commensalism, and parasitism, requiring various modifications to their body structure.

The head, or prostomium, is relatively well developed, compared with other annelids. It projects forward over the mouth, which therefore lies on the animal's underside. The head normally includes two to four pair of eyes, although there are some blind species. These are typically fairly simple structures, capable of distinguishing only light and dark, although some species have large eyes with lenses that may be capable of more sophisticated vision.

The head also includes a pair of antennae, tentacle-like palps, and a pair of pits lined with cilia, known as "nuchal organs". These latter appear to be chemoreceptors, and help the worm to seek out food.

Internal anatomy and physiology



General anatomy of a polychaete

The outer surface of the body wall consists of a simple columnar epithelium covered by a thin cuticle. Underneath this, in order, are a thin layer of connective tissue, a layer of circular muscle, a layer of longitudinal muscle, and a peritoneum surrounding the body cavity. Additional oblique muscles move the parapodia. In most species, the body cavity is divided into separate compartments by sheets of peritoneum between each segment, but in some species, it is more continuous.

The mouth of polychaetes varies in form depending on their diet, since the group includes predators, herbivores, filter feeders, scavengers, and parasites. In general, however, it possesses a pair of jaws and a pharynx that can be rapidly everted, allowing the worm to grab food and pull it into the mouth. In some species, the pharynx is modified into a lengthy proboscis. The digestive tract is a simple tube, usually with a stomach part way along.

The smallest species, and those adapted to burrowing, lack gills, breathing only through their body surface. Most other species, however, have external gills, generally, although not always, associated with the parapodia.

There is usually a well-developed, if simple, circulatory system. There are two main blood vessels, with smaller vessels to supply the parapodia and the gut. Blood flows forward in the dorsal vessel, above the gut, and returns back down the body in the ventral vessel, beneath the gut. The blood vessels themselves are contractile, helping to push the blood along, so most species have no need of a heart. In a few cases, however, muscular pumps analogous to a heart are found in various parts of the system. Conversely, some species have little or no circulatory system at all, transporting oxygen in the coelomic fluid that fills their body cavity.

The blood itself may be colourless, or have any of three different respiratory pigments. The most common of these is haemoglobin, but some groups have haemerythrin or the green-coloured chlorocruorin instead.

The nervous system consists of a single or double ventral nerve cord running the length of the body, with ganglia and a series of small nerves in each segment. The brain is relatively large, compared with that of other annelids, and lies in the upper part of the head. An endocrine gland is attached to the ventral posterior surface of the brain, and appears to be involved in reproductive activity. In addition to the sensory organs on the head, there may also photosensitive eye-spots on the body, statocysts, and numerous additional sensory nerve endings, most likely in involved with the sense of touch.

Polychaetes have a varying number of protonephridia or metanephridia for excreting waste, which in some cases can be relatively complex in structure. The body also contains greenish "chloragogen" tissue, similar to that found in oligochaetes, which appears to function in metabolism, in a similar fashion to that of the vertebrate liver.

Their cuticle is constructed from cross-linked fibres of collagen and may be 200 nm to 13mm thick. Their jaws are formed from sclerotised collagen, and their setae from sclerotised chitin.

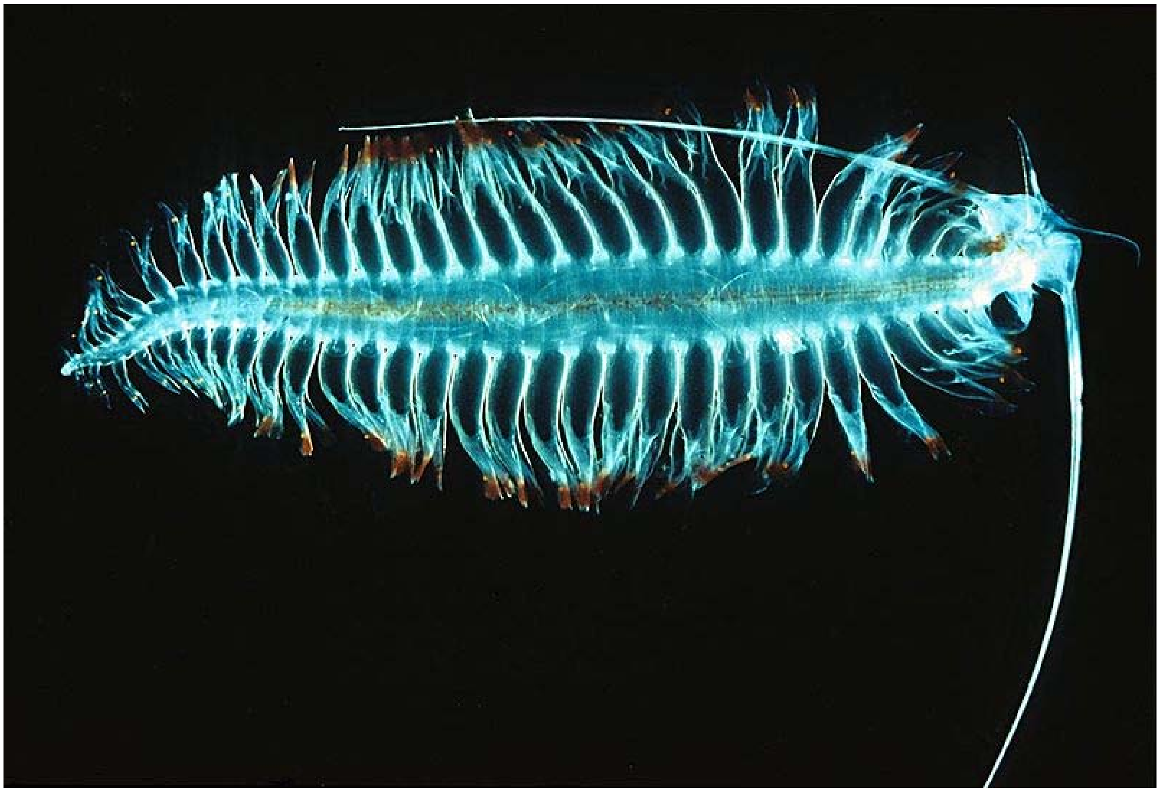
Ecology

Christmas tree worms (*Spirobranchus giganteus*) from East Timor.

Polychaetes are extremely variable in both form and lifestyle and include a few taxa that swim among the plankton. Most burrow or build tubes in the sediment, and some live as commensals. A few are parasitic. The mobile forms (Errantia) tend to have well-developed sense organs and jaws, while the stationary forms (Sedentaria) lack them but may have specialized gills or tentacles used for respiration and deposit or filter feeding, e.g., fanworms.

A few groups have evolved to live in terrestrial environments, like Namanereidinae with many terrestrial species, but are restricted to humid areas. Some have even evolved cutaneous invaginations for aerial gas exchange.

Sabellastarte indica



Tomopteris from plankton

Notable polychaetes

- One notable polychaete, the Pompeii worm (*Alvinella pompejana*) is endemic to the hydrothermal vents of the Pacific Ocean. Pompeii worms are among the most heat-tolerant complex animals known.
- A recently discovered genus, *Osedax*, includes a species nicknamed the "bone-eating snot flower".
- Another remarkable polychaete is *Hesiocaeca methanicola*, which lives on methane clathrate deposits.
- *Lamellibrachia luymesi* is a cold seep tube worm that reaches lengths of over 3 meters and may be the most long-lived animal at over 250 years old.
- A still unclassified multi-legged predatory polychaete worm was identified only by observation from the underwater vehicle Nareus at the bottom of the Challenger Deep, the greatest depth in the oceans, near 10,902 m (35,768 ft) depth. It was about an inch long visually, but the probe failed to capture it, so it could not be studied in detail.

Reproduction

Most polychaetes have separate sexes, rather than being hermaphroditic. The most primitive species have a pair of gonads in every segment, but, in most species, there has been some degree of specialisation. The gonads shed immature gametes directly into the body cavity, where they complete their development. Once mature, the gametes are shed into the surrounding water through ducts or openings that vary between species, or in some cases by the complete rupture of the body wall (and subsequent death of the adult). A few species copulate, but most fertilise the eggs externally.

The fertilised eggs typically hatch into trochophore larvae, which float among the plankton, and eventually metamorphose into the adult form by adding segments. A few species have no larval form, with the egg hatching into a form resembling the adult, and in many that do have larvae, the trochophore never feeds, surviving off the yolk that remains from the egg.

Some of the polychaetes exhibit remarkable reproductive strategies. Some species in the genus *Eunicie* reproduce by a process called epitoky. For much of the year, these worms look like any other burrow-dwelling polychaete, but as the breeding season approaches the worm undergoes a remarkable transformation as new, specialized segments begin to grow from its rear end until the worm can be clearly divided into two halves. The front half, the atoke, is asexual. The new rear half is responsible for breeding and is known as the epitoke.

Each of the epitoke segments is packed with eggs and sperm and features a single eyespot on its surface. The beginning of the last lunar quarter is the cue for these animals to breed and the epitokes break free from the atokes and float to the surface. The eye spots sense when the epitoke reaches the surface and the segments from millions of worms burst, releasing their eggs and sperm into the water.

Fossil record

Tube of a serpulid worm attached to a branch of the coral *Cladocora* from the Pliocene of Cyprus.

The oldest crown-group polychaete fossils come from the Sirius Passet Lagerstatte, a rich, sedimentary deposit in Greenland tentatively dated to the late Atdabanian (early Cambrian). Many of the more famous Burgess Shale organisms, such as *Canadia* and *Wiwaxia*, may also have polychaete affinites. An even older fossil, *Cloudina*, dates to the terminal Ediacaran period; this has been interpreted as an early polychaete, although consensus is absent.

Being soft bodied, the fossil record of polychaetes is dominated by their fossilized jaws, known as scolecodonts, and the mineralized tubes that some of them secrete. However, their cuticle does have some preservation potential; it tends to survive for at least 30 days after a polychaete's death. Although biomineralisation is usually necessary to preserve soft tissue after this time, the presence of polychaete muscle in the non-mineralised Burgess shale shows that this need not always be the case. Their preservation potential is similar to that of jellyfish.

Taxonomy and systematics

Taxonomically, polychaetes are thought to be paraphyletic, meaning that the group contains its most recent common ancestor, but does not contain all descendants of that ancestor. Groups that may be descended from the polychaetes include the earthworms, leeches, sipunculans, and echiurans. The Pogonophora and Vestimentifera were once considered separate phyla, but are now classified in the polychaete family Siboglinidae.

Much of the classification below matches Rouse & Fauchald, 1998, although that paper does not apply ranks above family.

Older classifications recognize many more (sub)orders than the layout presented here. As comparatively few polychaete taxa have been subject to cladistic analysis, some groups which are usually considered invalid today may eventually be reinstated.

- **Subclass Palpata**
    - Order Aciculata
        - Basal or *incertae sedis*
            - Family Aberrantidae
            - Family Nerillidae
            - Family Spintheridae
        - Suborder Eunicida
            - Family Amphinomidae
            - Family Diurodrilidae
            - Family Dorvilleidae
            - Family Eunicidae
            - Family Euphrosinidae
            - Family Hartmaniellidae
            - Family Histriobdellidae
            - Family Lumbrineridae
            - Family Oenonidae
            - Family Onuphidae
        - Suborder Phyllodocida
            - Family Acoetidae
            - Family Alciopidae
            - Family Aphroditidae
            - Family Chrysopetalidae
            - Family Eulepethidae
            - Family Glyceridae
            - Family Goniadidae
            - Family Hesionidae
            - Family Ichthyotomidae
            - Family Iospilidae
            - Family Lacydoniidae
            - Family Lopadorhynchidae
            - Family Myzostomatidae

        - Family Nautillienellidae
        - Family Nephtyidae
        - Family Nereididae
        - Family Paralacydoniidae
        - Family Pholoidae
        - Family Phyllodocidae
        - Family Pilargidae
        - Family Pisionidae
        - Family Polynoidae
        - Family Pontodoridae
        - Family Sigalionidae
        - Family Sphaeodoridae
        - Family Syllidae
        - Family Typhloscolecidae
        - Family Tomopteridae
- Order Canalipalpata
    - Basal or *incertae sedis*
        - Family Polygordiidae
        - Family Protodrilidae
        - Family Protodriloididae
        - Family Saccocirridae
    - Suborder Sabellida
        - Family Oweniidae
        - Family Siboglinidae (formerly the phyla Pogonophora & Vestimentifera)
        - Family Serpulidae
        - Family Sabellidae
        - Family Sabellariidae
        - Family Spirorbidae
    - Suborder Spionida
        - Family Apistobranchidae
        - Family Chaetopteridae
        - Family Longosomatidae
        - Family Magelonidae
        - Family Poecilochaetidae
        - Family Spionidae
        - Family Trochochaetidae
        - Family Uncispionidae
    - Suborder Terebellida
        - Family Acrocirridae (sometimes placed in Spionida)
        - Family Alvinellidae
        - Family Ampharetidae
        - Family Cirratulidae (sometimes placed in Spionida)
        - Family Ctenodrilidae (sometimes own suborder Ctenodrilida)

        - Family Fauveliopsidae (sometimes own suborder Fauveliopsida)
        - Family Flabelligeridae (sometimes suborder Flabelligerida)
        - Family Flotidae (sometimes included in Flabelligeridae)
        - Family Pectinariidae
        - Family Poeobiidae (sometimes own suborder Poeobiida or included in Flabelligerida)
        - Family Sternaspidae (sometimes own suborder Sternaspida)
        - Family Terebellidae
        - Family Trichobranchidae
- **Subclass Scolecida**
    - Family Aeolosomatidae
    - Family Arenicolidae
    - Family Capitellidae
    - Family Cossunidae
    - Family Maldanidae
    - Family Opheliidae
    - Family Orbiniidae
    - Family Paraonidae
    - Family Parergodrilidae
    - Family Potamodrilidae
    - Family Psammodrilidae
    - Family Questidae
    - Family Scalibregmatidae

2. Clitellata

Clitellata	
	
Earthworm	
Scientific classification	
Kingdom:	Animalia
Phylum:	Annelida
Class:	**Clitellata**
Subclasses	
Branchiobdellae Hirudinea "Oligochaeta" (paraphyletic)	

Clitellata is a class of Annelid worms, characterized by having a clitellum - the 'collar' that forms a reproductive cocoon during part of their life cycle. The **clitellates** comprise around 8,000 species. Unlike the class of Polychaeta, they do not have parapodia and their heads are less developed.

Habitats

Most clitellates live on land, in freshwater and in the ocean.

Reproduction

All clitellata are hermaphrodites. During reproduction, the clitellum secretes a coat which hardens. The worm then creeps out backward from the coat and deposits either fertilized zygotes or both ovae and sperms into the coat, which is then packed into a cocoon. The zygotes then evolve further directly in the cocoon without passing through a larva stadium (as opposed to other annelids, e.g. polychaeta.) This mechanism is considered to be apomorphic (newer in evolution).

Systematics

- Branchiobdella - formerly in Hirudinea
- Hirudinea (leeches)
- Oligochaeta (earthworms - aquatic microdriles + terrestrial megadriles)

The Acanthobdellidea are sometimes moved out of the Hirudinea as a distinct subclass too. Overall. clitellate phylogeny is not well resolved.

Namely, the Acanthobdellidea, Branchiobdella and Hirudinea are monophyletic but actually embedded among the "Oligochaeta", which are actually an evolutionary grade of lineages that are outwardly similar but not actually very close relatives. In particular, the leeches and earthworms appear to be very close relatives. Two approaches are possible:

- abolish Oligochaeta as traditionally delimited in favor of a number of smaller monophyletic lineages
- treat Oligochaeta and Clitellata as synonymous while splitting up the traditional "oligochaetes" into monophyletic lineages.

3. Oligochaeta

Oligochaeta

Earthworm (*Lumbricus terrestris*)

Scientific classification	
Kingdom:	Animalia
Phylum:	Annelida
Class:	Clitellata
Subclass:	**Oligochaeta**
Orders	
Haplotaxida Lumbriculida Moniligastrida	

Oligochaeta (singular **Oligochaete**, is a subclass of animals in the biological phylum Annelida, which is made up of many types of aquatic and terrestrial worms, and this includes all of the various earthworms. Specifically, it contains the terrestrial megadrile earthworms (some of which are semi- or fully aquatic), and freshwater or semi-terrestrial microdrile forms including the tubificids, pot worms and ice worms (Enchytraeidae), blackworms (Lumbriculidae) and several interstitial marine worms.

With around 10,000 known species the Oligochaeta make up about one half of the phylum Annelida.

These worms usually have few setae (chaetae) or "bristles" on the outer body surface, and lack parapodia, unlike polychaeta.

Common characteristics

Oligochaetes are well-segmented worms and most have a spacious body cavity (coelom) that is used as a hydroskeleton. They range in length from less than 0.5 millimetres (0.020 in) up to 2 to 3 metres (6.6 to 9.8 ft) in the 'giant' species such as the giant Gippsland earthworm and the Mekong Worm *Amynthas mekongianus* (Cognetti, 1922).

The first segment, or prostomium, of oligochaetes is usually a smooth lobe or cone without sensory organs, although it is sometimes extended to form a tentacle. The remaining segments have no appendages, but they do have a small number of bristles, or setae. These tend to be longer in aquatic forms than in the burrowing earthworms, and can have a variety of shapes. Oligochaetes are able to reproduce via insertion of a penis into an orifice called a vagina.

Each segment has four bundles of setae, with two igloos on the underside, and the others on the sides. The bundles can contain anything from one to twenty-five setae, and include muscles to pull them in and out of the body. This enables the worm to gain a grip on the soil or mud as it burrows into the substrate. When burrowing, the body moves peristaltically, alternately contracting and stretching to push itself forward.

A number of segments in the forward part of the body are modified by the presence of numerous secretory glands. Together, they form the clitellum, which is important in reproduction.

Internal anatomy

Most Oligochaetes are detritus feeders, although some genera are predaceous, such as *Agriodrilus* and *Phagodrilus*. The digestive tract is essentially a tube running the length of the body, but has a powerful muscular pharynx immediately behind the mouth cavity. In many species, the pharynx simply helps the worm suck in food, but in many aquatic species, it can be turned inside out and placed over food like a suction cup before being pulled back in.

The remainder of the digestive tract may include a crop for storage of food, and a gizzard for grinding it up, although these are not present in all species. The oesophagus includes "calciferous glands" that maintain calcium balance by excreting indigestible calcium carbonate into the gut. A number of yellowish "chloragogen cells" surround the intestine and the dorsal blood vessel, forming a tissue that functions in a similar fashion to the vertebrate liver. Some of these cells also float freely in the body cavity, where they are referred to as "eleocytes".

Most oligochaetes have no gills or similar structures, and simply breathe through their moist skin. The few exceptions generally have simple, filamentous gills. Excretion is through small ducts known as metanephridia. Terrestrial oligochaetes secrete urea, but the aquatic forms typically secrete ammonia, which dissolves rapidly into the water.

The vascular system consists of two main vessels connected by lateral vessels in each segment. Blood is carried forward in the dorsal vessel (in the upper part of the body) and back through the ventral vessel (underneath), before passing into a sinus surrounding the intestine. Some of the smaller vessels are muscular, effectively forming hearts; from one to five pairs of such hearts is typical. The blood of oligochaetes contains haemoglobin in all but the smallest of species, which have no need of respiratory pigments.

The nervous system consists of two ventral nerve cords, which are usually fused into a single structure, and three to four pairs of smaller nerves per body segment. Only a few aquatic oligochaetes have eyes, and even then they are only simply ocelli. Nonetheless, their skin has several individual photoreceptors, allowing the worm to sense the presence of light, and burrow away from it. Oligochaetes can taste their surroundings using chemoreceptors located in tubercles across their body, and their skin is also supplied with numerous free nerve endings that presumably contribute to their sense of touch.

Life cycle

Earthworms are hermaphrodites, which means that each animal has both male and female reproductive organs. They have external fertilization (except for some members of the African family Eudrilidae), but copulate and store sperm in a receptacle called a spermatheca. When two earthworms mate, both worms typically fertilize each other. Like leeches, they have a clitellum which secretes a "cocoon" or capsule into which both eggs and sperm are deposited and acts as an incubator for the embryonic worms. The cocoon is deposited in the soil. On hatching, the young worms resemble small adults and grow continually until they reach maturity. They lack a trochophore larval stage.

Habitat

Earthworms typically live in various types of soil or mud, as well as organic matter such as compost or even feces. They are found on every continent except Antarctica. Native earthworm species are often eradicated from natural areas as people clear native vegetation and introduced species become more dominant in these disturbed habitats. Introduced earthworms are most common in disturbed environments such as suburban gardens and farmland paddocks.

Families

The following list of Oligochaeta families follows ICZN conventionn so that family-group name (ending in -idae) is followed by authorship and date.

Oligochaete worm

- Randiellidae (Erséus & Strehlow, 1986)
- Tubificidae (Vejdovsky, 1884 (including Naidinae Ehrenberg, 1831))
- Narapidae (Righi, 1983)
- Opistocystidae (Cernosvitov, 1936)
- Dorydrilidae (Cook, 1971)
- Parvidrilidae (Erséus, 1999)
- Phreodrilidae (Beddard, 1891)
- Propappidae (Coates, 1986)
- Haplotaxidae (Michaelsen, 1900)
- Tiguassuidae (Brinkhurst, 1988)
- Lumbriculidae (Vejdovsky, 1884)
- Enchytraeidae (Vejdovsky, 1879)
- Moniligastridae (Claus, 1880)
- Alluroididae (Michaelsen, 1900)
- Syngenodrilidae (Smith and Green, 1919)
- Glossoscolecidae (Michaelsen, 1900)
- Tumakidae (Righi, 1995)
- Ailoscolecidae (Bouché, 1969) (including Komarekionidae Gates, 1974)
- Sparganophilidae (Michaelsen, 1918)
- Microchaetidae (Michaelsen, 1900)
- Lumbricidae Claus, 1876 (including Diporodrilinae Bouché, 1970; Eiseniinae Omodeo, 1956; Spermophorodrilinae Omodeo & Rota, 1989; Postandrilinae Qiu & Bouché, 1998; Allolobophorinae Kvavadze, 2000 and Helodrilinae Kvavadze, 2000)
- Kynotidae - Brinkhurst & Jamieson, 1971
- Hormogastridae Michaelsen, 1900 (including Vignysinae Bouché, 1970 and Xaninae Diaz Cosin *et al.*, 1989)
- Lutodrilidae McMahan, 1978
- Criodrilidae Vejdovsky, 1884 (including Biwadrilidae Brinkhurst & Jamieson, 1971)
- Almidae Duboscq, 1902
- Ocnerodrilidae Beddard, 1891 (including Malabariinae Gates, 1966)
- Acanthodrilidae Claus, 1880 (including Diplocardiinae Michaelsen, 1900)
- Octochaetidae Michaelsen, 1900 (including Benhamiinae Michaelsen, 1895/7)
- Exxidae Blakemore, 2000
- Megascolecidae Rosa, 1891 (including Pontodrilinae Vejdovsky, 1884; Plutellinae Vejdovsky, 1884 and Argilophilinae Fender & McKey-Fender, 1990)
- Eudrilidae Claus, 1880.

4. Leech

Leech	
	
Hirudo medicinalis	
Scientific classification	
Kingdom:	Animalia
Phylum:	Annelida
Class:	Clitellata
Subclass:	**Hirudinea** Lamarck, 1818
Infraclasses	
Acanthobdellidea Euhirudinea	

Leeches are annelids comprising the subclass **Hirudinea**. There are freshwater, terrestrial, and marine leeches. Like the Oligochaeta, they share the presence of a clitellum. Like earthworms, leeches are hermaphrodites. Some, but not all, leeches are hematophagous.

The European medical leech, *Hirudo medicinalis*, and some congeners, as well as some other species, have been used for clinical bloodletting for thousands of years, although most leeches do not feed on human blood, but instead prey on small invertebrates, which they eat whole.

Haemophagic leeches attach to their hosts and remain there until they become full, at which point they fall off to digest. A leech's body is composed of 34 segments. They all have an anterior (oral) sucker formed from the first six segments of their body, which is used to connect to a host for feeding, and also release an anesthetic to prevent the host from feeling the leech. They use a combination of mucus and suction (caused by concentric muscles in those six segments) to stay attached and secrete an anti-clotting enzyme, hirudin, into the host's blood stream.

Some species of leech will nurture their young, while providing food, transport, and protection, which is unusual behavior amongst annelids.

Systematics and taxonomy

Leeches are presumed to have evolved from certain Oligochaeta, most of which feed on detritus. However, some species in the Lumbriculidae are predatory and have similar adaptations as found in leeches. Consequently, the systematics and taxonomy of leeches is in need of review. While leeches form a clade, the remaining oligochetes are not their sister taxon but a diverse paraphyletic group containing some lineages that are closely related to leeches, and others that are far more distant.

There is some dispute as to whether Hirudinea should be a class itself, or a subclass of the Clitellata. The resolution mainly depends on the eventual fate of the oligochaetes, which as noted above do not form a natural group as traditionally circumscribed. Another possibility would be to include the leeches in the taxon Oligochaeta, which would then be ranked as a class and contain most of the clitellates. The Branchiobdellida are leechlike clitellates which were formerly included in the Hirudinea but are apparently just really close relatives.

Leech climbing a door by Lake Leake, Tasmania

The more primitive Acanthobdellidea are often included with the leeches, but some authors treat them as a separate clitellate group. True leeches of the infraclass

Euhirudinea have both anterior and posterior suckers. They are divided into two groups: Arhynchobdellida and Rhynchobdellida

- Rhynchobdellida): "Jawless" leeches, armed with a muscular straw-like proboscis puncturing organ in a retractable sheath. The Rhynchobdellae consist of two families:
    - Glossiphoniidae: Flattened leeches with a poorly defined anterior sucker
    - Piscicolida: have cylindrical bodies and a usually well-marked, bell-shaped, anterior sucker. The Glossiphoniidae live in fresh-water habitats; the Pisciolidae are found in seawater habitats.

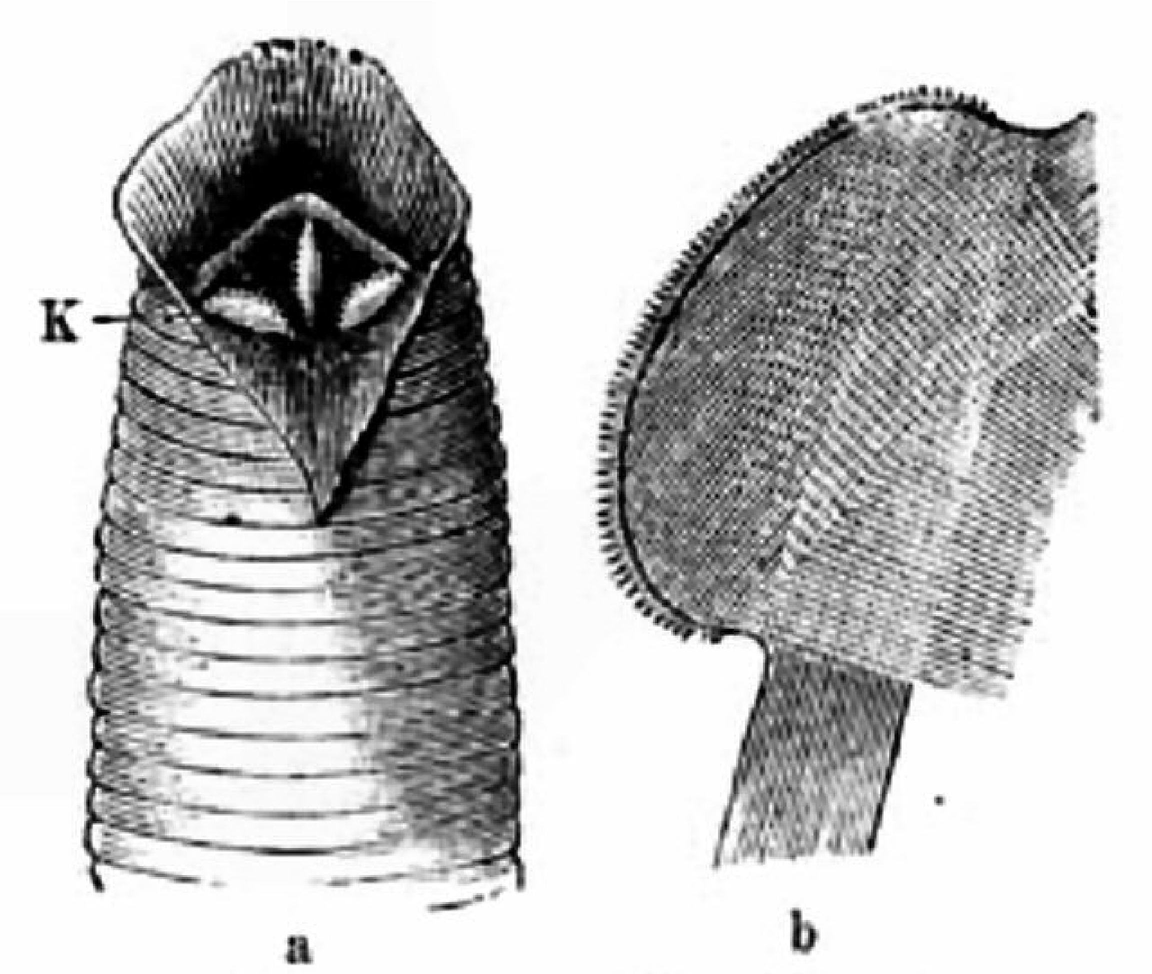
- Arhynchobdellida: Leeches which lack a proboscis and which may or may not have jaws armed with teeth. Arhynchobellids are divided into two orders:
    - Gnathobdela: In this order of "jawed" leeches, armed with teeth, is found the quintessential leech: the European medical (bloodsucking) leech, *Hirudo medicinalis*. It has a tripartite-jaw filled with hundreds of tiny sharp teeth. The incision mark left on the skin by the European medical leech is an inverted Y inside a circle. Its North American counterpart is *Macrobdela decora*, a much less efficient medical leech. Within this order, the family Hirudidae is characterized by aquatic leeches and the family Haemadipsidae by terrestrial leeches. In the latter are *Haemadipsa sylvestris*, the Indian leech and *Haemadipsa zeylanica* (yamabiru), the Japanese mountain or land leech.
    - Pharyngobdella: These so called worm-leeches consist of freshwater or amphibious leeches that have lost the ability to penetrate a host's tissue and suck blood. They are carnivorous and equipped with a relatively large, toothless, mouth to ingest worms or insect larvae, which are swallowed whole.
      The Pharyngobdella have six to eight pairs of eyes, as compared with five pairs in Gnathobdelliform leeches, and include three related families. The Erpobdellidae are some species from freshwater habitats.

Reproduction

Leeches are hermaphrodites, meaning each one of them has both female and male reproductive organs (ovaries and testes respectively). Leeches reproduce by reciprocal fertilization, and sperm transfer occurs during copulation. The leech exercising the role of the male will grow a sperm sack near the end of its tail, and the leech playing the female will bite it off, thus reproducing. Similarly to the earthworms, leeches also use a clitellum to hold their eggs and secrete the cocoon.

During reproduction leeches utilize hyperdermic injection of their sperm. They use a spermatophore, which is a structure containing the sperm. Once next to another leech, the two will line up with their anterior side opposite the other's posterior. The leech then shoots the spermatophore into the clitellur region of the opposing leech where its sperm will make its way to the female reproductive parts.

Nutrition



Mouthparts and sucker

A leech swollen with blood

Leech attacking a slug

On haematophagous leeches, the digestive system starts with the jaw which is located ventrally on the anterior side of the body. It is attached to the pharynx, then the esophagus extending to the crop, which leads to the intestinum, where it ends at the posterior sucker. The crop is a type of stomach that works like an expandable storage compartment. The crop allows a leech to store blood up to five times its body size; and because the leech produces an anti-coagulant, the stored blood remains in a liquid state; because of this ability to hold blood without the blood decaying, due to bacteria living inside the crop, medicinal leeches only need to feed two times a year.

The body of predatory leeches are similar, though some may also have a protrusible proboscis which is retracted in their mouth. Such leeches are often ambush predators, which lie in wait, and strike their prey using their proboscis in a spear-like fashion.

It was long thought that bacteria in the gut carried on digestion for the leech instead of endogenous enzymes which are very low or absent in the intestine. Relatively recently it has been discovered that all leeches and leech species studied do produce endogenous intestinal exopeptidases, which can unlink free terminal-end amino acids, one amino acid monomer at a time, from a gradually unwinding and degrading protein polymer. However, unzipping of the protein can start from either the amino (tail) or carboxyl (head) terminal-end of the protein molecule. It just so happens that the leech exopeptidase (arylamidases), possibly aided by proteases from endosymbiotic bacteria in the intestine, starts from the tail or amino protein, free-end, slowly but progressively removing many hundreds of individual terminal amino acids for resynthesis into proteins that constitute the leech. Since leeches lack endopeptidases, the mechanism of protein digestion can not follow the same sequence as it would in all other animals where exopeptidases act sequentially on peptides produced by the action of endopeptidases. Exopeptidases are especially prominent in the common North American worm-leech *Erpobdella punctata*. This evolutionary choice of exopeptic digestion in Hirudinea distinguishes these carnivorous clitellates from Oligochaeta.

Deficiency of digestive enzymes (except exopeptidases) but more importantly deficiency of vitamins, B complex for example, in leeches is compensated for by enzymes and vitamins produced by endosymbiotic microflora. In *Hirudo medicinalis* these supplementary factors are produced by an obligatory symbiotic relationship with two bacterial species, *Aeromonas veronii* and a still uncharacterized *Rikenella* species. Non-bloodsucking leeches such as *Erpobdella punctata* are host to three bacterial symbionts, *Pseudomonas sp.*, *Aeromonas sp.*, and *Klebsiella sp.* (a slime producer). The bacteria are passed from parent to offspring in the cocoon as it is formed.

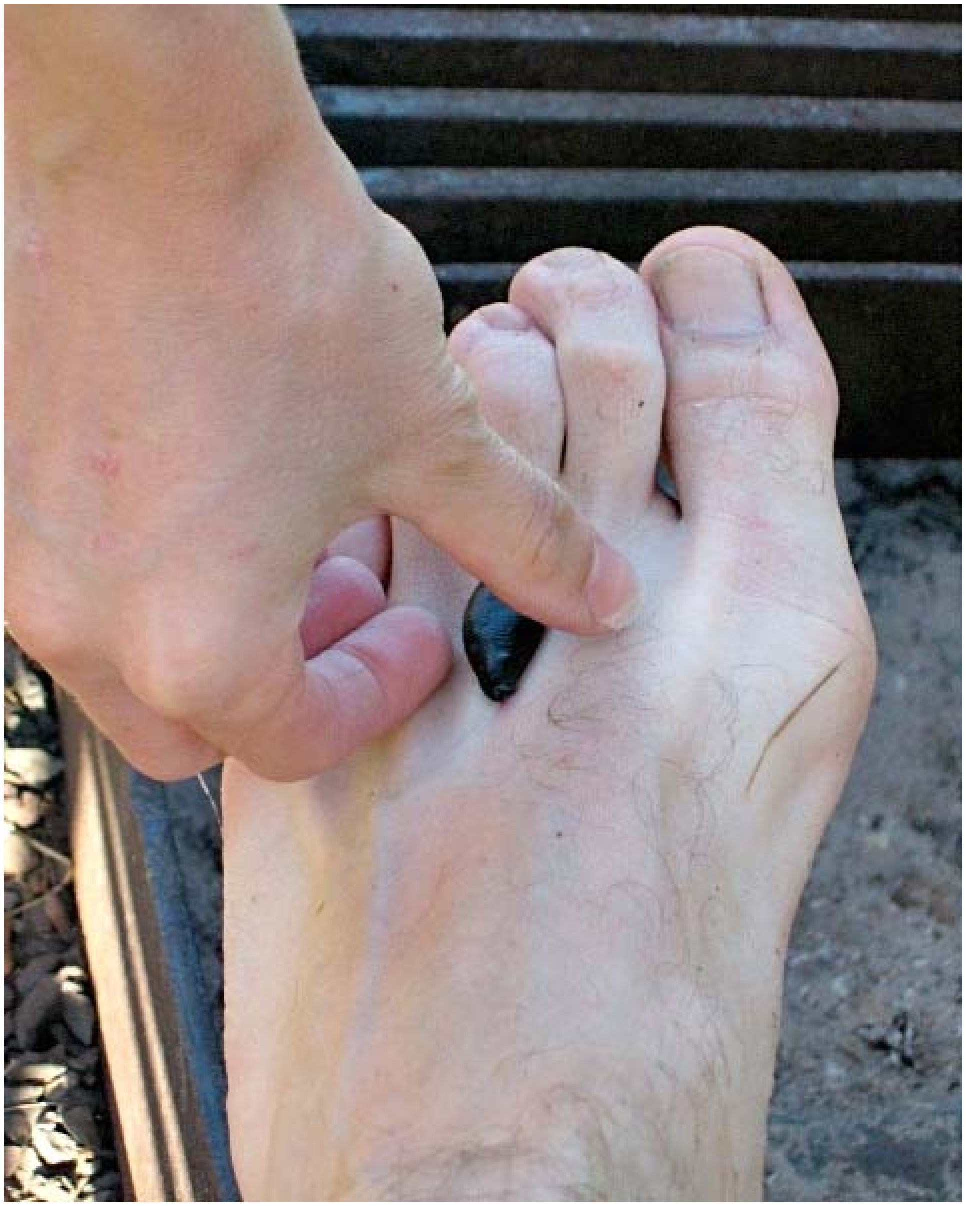
Leech bites

Effects

Though certain species of leeches feed on blood, not all species can bite; 90% of them solely feed off decomposing bodies and open wounds of amphibians, reptiles, waterfowl, fish, and mammals (including, but not limited to, humans). A leech attaches itself when it bites, and it will stay attached until it has had its fill of blood. Due to an anticoagulant (hirudin) that leeches secrete, bites may bleed more than a normal wound after the leech is removed. The effect of the anticoagulant will wear off several hours after the leech is removed and the wound is cleaned.

Leeches normally carry parasites in their digestive tract which cannot survive in humans and do not pose a threat. However, bacteria, viruses, and parasites from previous blood sources can survive within a leech for months, and may be retransmitted to humans. A study found both HIV and hepatitis B in African leeches from Cameroon.

Removal



Hand removing a land leech—since they do not burrow into the skin nor the head in the wound. A sore develops and lasts for about a week. Grande Ronde River, Oregon (U.S.)

One recommended method of removal is using a fingernail or other flat, blunt object to break the seal of the oral sucker at the anterior end (the smaller, thinner end) of the leech, repeating with the posterior end, then flicking the leech away. As the fingernail is pushed along the person's skin against the leech, the suction of the sucker's seal is broken, at which point the leech should detach its jaws.

A common but medically inadvisable technique to remove a leech is to apply a flame, a lit cigarette, salt, soap, or a chemical such as alcohol, vinegar, lemon juice, insect repellent, heat rub, or certain carbonated drinks. These cause the leech to regurgitate its stomach contents into the wound and quickly detach. However, the vomit may carry disease, and thus increase the risk of infection.

An externally attached leech will detach and fall off on its own when it is satiated on blood, usually in about 20 minutes (but will stay there for as long as it can). Internal attachments, such as nasal passage or vaginal attachments, are more likely to require medical intervention.

Treatment

After removal or detachment, the wound should be cleaned with soap and water, and bandaged. Bleeding may continue for some time, due to the leech's anti-clotting enzyme. Applying pressure can reduce bleeding, although blood loss from a single bite is not dangerous. The wound normally itches as it heals, but should not be scratched as this may complicate healing and introduce other infections. An antihistamine can reduce itching, and applying a cold pack can reduce pain or swelling.

Some people suffer severe allergic or anaphylactic reactions from leech bites, and require urgent medical care. Symptoms include red blotches or an itchy rash over the body, swelling away from the bitten area (especially around the lips or eyes), feeling faint or dizzy, and difficulty breathing.

Prevention

There is no guaranteed method of preventing leech bites in leech-infested areas. The most reliable method is to cover exposed skin. The effect of insect repellents is disputed, but it is generally accepted that strong (maximum strength or tropical) insect repellents do help prevent bites.

Leech socks can be helpful in preventing bites when the full body will not be at risk of contact with leeches. Leech socks are pulled over the wearer's trousers to prevent leeches reaching the exposed skin of the legs and attaching there or climbing towards the torso. The socks are generally a light color that also makes it easier to spot leeches climbing up from the feet and looking for skin to attach to.

There are many home remedies to help prevent leech bites. Many people have a great deal of faith in these methods, but none of them have been proven effective. Some home remedies include: a dried residue of bath soap, tobacco leaves between the toes, pastes of salt or baking soda, citrus juice, Neem oil and eucalyptus oil. Diluted calcium hydroxide may also be used as a repellent, but may be damaging or irritating to the skin. One other remedy commonly practiced in the western ghats of southern India is castor oil mixed with snuff powder, or powdered tobacco.

Hirudotherapy

The term refers to the use of leeches in medicine.

The use of leeches in medicine dates as far back as 2,500 years ago when they were used for bloodletting in ancient India. Leech therapy is explained in ancient Ayurvedic texts. Many ancient civilizations practiced bloodletting including Indian and Greek civilizations. In ancient Greek history, bloodletting was practiced according to the humoral theory, which proposed that when the four humors, blood, phlegm, black and yellow bile in the human body were in balance, good health was guaranteed. An imbalance in the proportions of these humors was believed to be the cause of ill health. Records of this theory were found in the Greek philosopher Hippocrates' collection in the fifth century B.C. Bloodletting using leeches was one method used by physicians to balance the humors and to rid the body of the plethora.

The use of leeches in modern medicine made its comeback in the 1980s after years of decline, with the advent of microsurgery such as plastic and reconstructive surgeries. In operations such as these, one problem that arises is venous congestion due to inefficient venous drainage. Sometimes because of the technical difficulties in forming an anastomosis of a vein, no attempt is made to re-attach a venous supply to a flap at all. This condition is known as venous insufficiency. If this congestion is not cleared up quickly, the blood will clot, arteries that bring the tissues their necessary nourishment will become plugged and the tissues will die. To prevent this leeches are applied to a congested flap and a certain amount of excess blood is consumed before the leech falls away. The wound will also continue to bleed for a while due to the anticoagulant (hirudin) in the leeches' saliva. The combined effect is to reduce the swelling in the tissues and promoting healing by allowing fresh, oxygenated blood to reach the area.

The active anticoagulant principle of leech saliva, is a small protein, hirudin. Discovery and isolation of this protein led to a method of producing it by recombinant technology. Recombinant hirudin is available to physicians as an intravenous anticoagulant preparation for injection, particularly useful for patients who are allergic to or cannot tolerate heparin.

Embryonic development

The first cleavage during early embryonic development in leech occurs at stage 2. This cleavage gives rise to an AB and a CD blastomere and is in the interphase of this cell division when a yolk-free cytoplasm called teloplasm is formed. The teloplasm is known to be a determinant for the specification of the D cell fate. In stage 3, during the second cleavage, an unequal division occurs in the CD blastomere. As a consequence, it creates a big D cell on the left and a smaller C cell to the right. This unequal division process is dependent on actinomycin, and by the end of stage 3 the AB cell divides. On stage 4 of development, the micromeres and teloblast stem cells are formed and subsequently, the D quadrant divides to form the DM and the DNOPQ teloblast precursor cells. By the end stage 6, the zygote contains a set of 25 micromeres, 3 macromeres (A, B and C) and 10 teloblasts derived from the D quadrant.

The teloblast are pairs of five different types (M, N, O, P and Q) of embryonic stem cells that form segmented columns of cells (germinal-band) in the surface of the embryo. The M-derived cells make mesoderm and some small set of neurons, N results in neural tissues and some ventral ectoderm, Q contributes to the dorsal ectoderm and O and P in the leech are equipotent cells (same developmental potential) that produce lateral ectoderm; however the difference between the two of them is that P creates bigger batches of dorso-lateral epidermis than O. The sludgeworm *Tubifex*, unlike the leech, specifies the O and P lineages early in development and therefore, these two cells are not equipotent. Each segment of the body of the leech is generated from one M, O, P cell types and two N and two Q cells types.

The ectoderm and mesoderm of the body trunk is exclusively derived from the teloblast cells in a region called posterior progress zone. The head of the leech that come from a non-segmented region, is formed by the first set of micromeres derived from A, B, C and D cells, keeping the bilateral symmetry between the AD and BC cells.

5. Siboglinidae

Siboglinidae

Riftia pachyptila

Scientific classification

Kingdom:	Animalia
Subkingdom:	Eumetazoa

Phylum:	Annelida
Class:	Polychaeta
Subclass:	Palpata
Order:	Canalipalpata
Family:	**Siboglinidae** Caullery, 1914

Siboglinidae, also known as the **beard worms**, is a family of polychaete annelid worms whose members made up the former phyla **Pogonophora** (the giant tube worms) and **Vestimentifera**. They are composed of about 100 species of vermiform creatures and live in thin tubes buried in sediments at ocean depths from 100 to 10,000 m. They can also be found in association with hydrothermal vents, methane seeps, with sunken plant material or whale carcasses.

The first specimen was dredged from the waters of what is now Indonesia in 1900. These specimens were given to French zoologist Maurice Caullery, who studied them for nearly 50 years.

Anatomy

Most siboglinids are less than 1 millimetre (0.04 in) in diameter but 10 to 75 centimetres (3.9 to 30 in) in length. They inhabit tubular structures composed of chitin and fixed to the bottom. The tubes are often clustered together in large colonies.

The body is divided into four regions. The anterior end is called the cephalic lobe, which bears from 1 to over 200 thin branchial ciliated tentacles, each bearing tiny side branches known as pinnules. Behind this is a glandular forepart, which helps to secrete the tube. The main part of the body is the trunk, which is greatly elongated and bears various annuli, papillae, and ciliary tracts. Posterior to the trunk is the short metamerically segmented opisthosoma, bearing external paired chaetae, which apparently help to anchor the animal to the base of its tube.

The body cavity has a separate compartment in each of the first three regions of the body, and extends into the tentacles. The opisthoma has a coelomic chamber in each of its 5 to 23 segments, separated by septa. The worms have a complex closed circulatory system and a well developed nervous system, but as adults, siboglinids completely lack a mouth, gut and anus.

Siboglinids are dioecious, with one gonad on each side of the trunk, within the body cavity. The fertilised eggs develop within the tubes, and hatch to produce small ciliated worm-like larvae.

Vestimentiferans

Like other tube worms, vestimentiferans are marine and benthic. *Riftia pachyptila*, a vestimentiferan, is known only from the hydrothermal vent systems. The vestimentiferans possess an anterior first body part called the obturaculum. Their main trunk of the body bears winglike extensions, the vestimentum, from which their name is derived. Also, unlike other siboglinids that never have a digestive tract, they have one that they completely lose during metamorphosis. Their primary nutrition is derived from the sulphide-rich fluids emanating from the hydrothermal vents they live by. The sulphides are metabolized by symbiotic hydrogen sulfide- or methane-oxidizing bacteria living in an internal organ, the trophosome. One gram of trophosome tissue can contain one billion bacteria. It is not completely understood how the worms instigate their relationship with the bacteria. One theory is that the very young worm has a vent on its body permitting the entry of the bacteria from the water. A more recent study of three species of tubeworms including *Riftia pachyptila* demonstrated that the bacteria actually infect juvenile worms through their skin. Their body is divided into four regions; the obturaculum, vestimentum, trunk, and opisthosome.

Genera in the family Siboglinidae

- *Birsteinia*
- *Choanophorus*
- *Cyclobrachia*
- *Lamellibrachia*
- *Lamellisabella*
- *Osedax*
- *Paraescarpia*
- *Ridgeia*
- *Riftia*
- *Siboglinoides*
- *Siboglinum*
- *Volvobrachia*

6. Echiura

Echiura
Temporal range: Upper Carboniferous–Recent

Bonellia viridis, female

Scientific classification

Kingdom:	Animalia
Phylum:	Annelida
Class:	**Echiura** Newby, 1940

Orders

Echiuroidea
Heteromyota
Xenopneusta

The **Echiura**, or spoon worms, are a small group of marine animals. They are often considered to be a group of annelids, although they lack the segmented structure found in other members of that group, and so may also be treated as a separate phylum. However, phylogenetic analyses of DNA sequences place echiurans and pogonophorans within the Annelida. The Echiura fossilise poorly and the earliest known specimen is from the Upper Carboniferous (called the Pennsylvanian in North America). However, U-shaped fossil burrows that could be Echiuran have been found dating back to the Cambrian.

Echiurans are marine worms similar in size and habit to sipunculans. Many genera, such as *Echiurus*, *Urechis*, and *Ikeda*, live in burrows in sand and mud; others live in rock and coral crevices. One species, *Thalassema mellita*, which lives off the southeastern coast of the US, inhabits the tests (exoskeleton) of dead sand dollars. When the worm is very small, it enters the test and later becomes too large to leave.

The majority of echiurans live in shallow water, but there are also deep sea forms. About 140 species have been described.

Anatomy

Echiura at a market in South Korea

Echiurans have a worm-like body with a large flattened proboscis projecting forward from the head. The body is typically drab in colour, but bright red and green species are known. The proboscis is a sheet-like structure, rolled around into a cylindrical tube with an open gutter at the ventral surface. The length of the proboscis varies greatly between species, and in some species is many times longer than the rest of the body. It is probably homologous with the prostomium of other annelids.

Compared with other annelids, echiurans have relatively few setae. In most species, there are just two, located on the underside of the body just behind the proboscis. In others, such as *Echiurus*, there are also further setae near the posterior end of the animal. Unlike other annelids, adult echiurans have no trace of segmentation.

The digestive system consists of a simple tube running the length of the body, with the anus being at the posterior end. The tube, however, is highly coiled, giving it a considerable length in relation to the size of the animal. A pair of simple or branched diverticula are connected to the rectum. These are lined with numerous minute ciliated funnels that open directly into the body cavity, and are presumed to be excretory organs.

Although some species lack a blood vascular system, where it is present, it resembles that of other annelids. The blood is essentially colourless, although some haemoglobin-containing cells are present in the coelomic fluid of the main body cavity. There can be anything from one to over a hundred metanephridia for excreting nitrogenous waste, which typically open near the anterior end of the animal.

Echiruans do not have a distinct respiratory system, absorbing oxygen through the body wall.

The nervous system consists of a brain near the base of the proboscis, and a ventral nerve cord running the length of the body. Aside from the absence of segmentation, this is a a similar arrangement to that of other annelids. Echiurans do not have any eyes or other distinct sense organs.

Feeding

Typical spoon worms, including *Bonellia*, are suspension feeders, projecting their proboscis out of their burrows, with the gutter projecting upwards. Edible particles will then settle onto the proboscis and a ciliated channel conducts the food to the trunk.

Perhaps the most remarkable feeding adaptations among the spoon worms can be seen in *Urechis*. *U. caupo* lives in a large, U-shaped burrow and by pulsating its body it drives water through its lair. To feed, it produces a conical mucus net that lines the burrow as water is sucked in at a rate of about 18L per hour. Edible particles are caught on the net, and after some time the worm slowly eats the net and all the edible matter sticking to it.

Reproduction

Echiruans are dioecious, with separate male and female individuals. The gonads are associated with the peritoneal membrane lining the body cavity, into which they release the gametes. The sperm and eggs complete their maturation in the body cavity, before being released into the surrounding water through the metanephridia. Fertilisation is external.

The species *Bonellia viridis*, also remarkable for the possible antibiotic properties of bonellin, the green chemical in its skin, is unusual for its extreme sexual dimorphism. Females are typically 8 centimetres (3.1 in) in body length, excluding the proboscis, but the males are only 1 to 3 millimetres (0.039 to 0.12 in) long, and spend their lives within the uterus of the female.

Fertilized eggs hatch into free-swimming trochophore larvae. In some species, the larva briefly develops a segmented body before transforming into the adult body plan, supporting the theory that echiruans evolved from segmented ancestors resembling more typical annelids.

Chapter- 11

Major Sub-groups of Platyhelminthes

1. Turbellaria

Turbellaria

A marine species *Pseudobiceros bedfordi* (Bedford's Flatworm), a member of the Polycladida

Scientific classification	
Kingdom:	Animalia
Phylum:	Platyhelminthes
Class:	**Turbellaria** Ehrenberg, 1831

Orders

Catenulida
Haplopharyngida
Lecithoepitheliata

Macrostomida
Nemertodermata
Polycladida
Prolecithophora
Rhabdocoela
Seriata
Temnocephalida

The **Turbellaria** are one of the traditional sub-divisions of the phylum Platyhelminthes (flatworms), and include all the sub-groups that are not exclusively parasitic. There are about 4,500 species, which range from 1 mm (0.039 in) to 600 mm (24 in) in length. All the larger forms are flat with ribbon-like or leaf-like shapes, since their lack of respiratory and circulatory systems means that they have to rely on diffusion for internal transport of metabolites. However, many of the smaller forms are round in cross section. Most are predators, and all live in water or in moist terrestrial environments. Most forms reproduce sexually and with few exceptions all are simultaneous hermaphrodites.

The Acoelomorpha and the genus *Xenoturbella* were formerly included in the Turbellaria, but are no longer regarded as Platyhelminthes. All the exclusively parasitic Platyhelminthes form a monophyletic group Neodermata, and it is agreed that these are descended from one small sub-group within the free-living Platyhelminthes. Hence the "Turbellaria" as traditionally defined are paraphyletic.

Description

Traditional classifications divide the Platyhelminthes into four groups: Turbellaria and the wholly parasitic Trematoda, Monogenea and Cestoda. In this classification the Turbellaria include the Acoelomorpha (Acoela and Nemertodermatida). The name "Turbellaria" refers to the "whirlpools" of microscopic particles created close the skins of aquatic species by the movement of their cilia.

Features common to all Platyhelminthes

Platyhelminthes are bilaterally symmetrical animals, in other words their left and right sides are mirror images of each other; this also implies that they have distinct top and bottom surfaces and distinct head and tail ends. Like other bilaterians they have three main cell layers (it is triploblastic), while the radially symmetrical cnidarians and ctenophore have only two cell layers. Unlike most other bilaterians, platyhelminthes have no internal body cavity and are therefore described as acoelomates. They also lack specialized circulatory and respiratory organs

The lack of circulatory and respiratory organs limits platyhelminths to sizes and shapes that enable oxygen to reach and carbon dioxide to leave all parts of their bodies by simple diffusion. Hence many are microscopic and the large species have flat ribbon-like or leaf-like shapes. The guts of large species have many branches, so that nutrients can diffuse to all parts of the body. Respiration through the whole surface of the body makes platyhelminthes vulnerable to fluid loss, and restricts them to environments where dehydration is unlikely: sea and freshwater; moist terrestrial environments such as leaf litter or between grains of soil; and as parasites within other animals.

The space between the skin and gut is filled with mesenchyme, a connective tissue that is made of cells and reinforced by collagen fibers that act as a type of skeleton, providing attachment points for muscles. The mesenchyme contains all the internal organs and allows the passage of oxygen, nutrients and waste products. It consists of two main types of cell: fixed cells, some of which have fluid-filled vacuoles; and stem cells, which can transform into any other type of cell, and are used in regenerating tissues after injury or asexual reproduction.

Most platyhelminths have no anus and regurgitate undigested material through the mouth. However some long species have an anus and some with complex branched guts have more than one anus, since excretion only through the mouth would be difficult for them. The gut is lined with a single layer of endodermal cells which absorb and digest food. Some species break up and soften food first by secreting enzymes in the gut or the pharynx (throat).

All animals need to keep the concentration of dissolved substances in their body fluids at a fairly constant level. Internal parasites and free-living marine animals live in environments that have high concentrations of dissolved material, and generally let their tissues have the same level of concentration as the environment, while freshwater animals need to prevent their body fluids from becoming too dilute. Despite this difference in environments, most platyhelminths use the same system to control the level of concentration in their body fluids. Flame cells, so called because the beating of their flagella looks like a flickering candle flame, extract from the mesenchyme water that contains wastes and some re-usable material, and drive it into networks of tube cells which are lined with flagella and microvilli. The tube cells' flagella drive the water towards exits called nephridiopores, while their microvilli re-absorb re-usable materials and as much water as is needed to keep the body fluids at the right level of concentration. These combinations of flame cells and tubule cells are called protonephredia.

In all platyhelminths the nervous system is concentrated at the head end. Most species have rings of ganglia in the head and main nerve trunks running along their bodies.

Planarians are famous for their ability to regenerate if divided by cuts across their bodies. Experiments show that, in fragments that do not already have a head, a new head grows most quickly on those that were closest to the original head. This suggests that the growth of a head is controlled by a chemical whose concentration diminishes from head to tail.

Features specific to Turbelleria

The turbellarian *Pseudoceros dimidiatus*

Two turbellarians mating by penis fencing. Each has two penises, the white spikes on the undersides of their heads.

These have about 4,500 species, are mostly free-living, and range from 1 mm (0.039 in) to 600 mm (24 in) in length. Most are predators or scavengers, and terrestrial species are mostly nocturnal and live in shaded humid locations such as leaf litter or rotting wood. However some are symbiotes of other animals such as crustaceans, and some are parasites. Free-living turbellarians are mostly black, brown or gray, but some larger ones are brightly colored.

Turbellarians have no cuticle (external layer of organic but non-cellular material). In a few species the skin is a syncitium, a collection of cells with multiple nuclei and a single shared external membrane. However the skins of most species consist of a single layer of cells, each of which generally has multiple cilia (small mobile "hairs"), although in some large species the upper surface has no cilia. These skins are also covered with microvilli between the cilia. They have many glands, usually submerged in the muscle layers below the skin and connect to the surface by pores through which they secrete mucus, adhesives and other substances.

Small aquatic species use the cilia for locomotion, while larger ones use muscular movements of the whole body or of a specialized sole to creep or swim. Some are capable of burrowing, anchoring their rear ends at the bottom of the burrow and then stretching the head up to feed and then pulling it back down for safety. Some terrestrial species throw a thread of mucus which they use as a rope to climb from one leaf to another.

Some Turbelleria have spicular skeletons, giving the appearance of annulations.

Diet and digestion

The acoel *Convoluta roscoffensis* swallows cells of the green alga *Tetraselmis* and does not feed as an adult, presumably relying on the alge to provide nourishment as endosymbionts. In other acoels the gut is lined by a syncitium. These and some other turbellarians have a simple pharynx lined with cilia and generally feed by using cilia to sweep food particles and small prey into their mouths, which are usually in the middle of the underside.

Most other turbellarians are carnivorous, either preying on small invertebrates or protozoans, or scavenging on dead animals. A few feed on larger animals, including oysters and barnacles, which some, such as *Bdelloura*, are commensal on the gills of horseshoe crabs. These turbellarians usually have an eversible pharynx, in other words, one that can be extended by being turned inside-out, and the mouths of different species can be anywhere along the underside. The freshwater species *Microstomum caudatum* can open its mouth almost as wide as its body is long, to swallow prey as large as itself.

The intestine is lined by phagocytic cells which capture food particles that have already been partially digested by enzymes in the gut. Digestion is then completed within the phagocytic cells and the nutrients diffuse through the body.

Nervous system

Concentration of nervous tissue in the head region is least marked in the acoels, which have nerve nets rather like those of cnidarians and ctenophores, but densest around the head. In other turbellarians, a distinct brain is present, albeit relatively simple in structure. From the brain one to four pairs of nerve cords run along the length the body, with numerous smaller nerves branching off. The ventral pair of nerve cords are typically the largest, and, in many species, are the only ones present. Unlike more complex animals, such as annelids, there are no ganglia on the nerve cords, other than those forming the brain.

Most turbellarians have pigment-cup ocelli ("little eyes"), one pair in most species, but two or even three pairs in some. A few large species have many eyes in clusters over the brain, mounted on tentacles, or spaced uniformly round the edge of the body. The ocelli can only distinguish the direction from which light is coming and enable the animals to avoid it.

A few groups – mainly catenulids, acoelomorphs and seriates – have statocysts, fluid-filled chambers containing a small solid particle or, in a few groups, two. These statocysts are thought to be balance and acceleration sensors, as that is the function they perform in cnidarian medusae and in ctenophores. However turbellarian statocysts have no sensory cilia, and it is unknown how they sense the movements and positions of the solid particles.

Most species have ciliated touch-sensor cells scattered over their bodies, especially on tentacles and around the edges. Specialized cells in pits or grooves on the head are probably smell-sensors.

Reproduction

Many turbellarians clone themselves by tranverse or longitudinal division, and others, especially acoels, reproduce by budding. The planarian *Dugesia* is a well-known representative of class Turbellaria.

All turbellarians are simultaneous hermaphrodites, having both female and male reproductive cells, and fertilize eggs internally by copulation. Some of the larger aquatic species mate by penis fencing, a duel in which each tries to impregnate the other, and the loser adopts the female role of developing the eggs.

Although the acoels have no distinct gonads at all, in other turbellarians there are one or more pairs of both testes and ovaries. Sperm ducts run from the testes, through bulb-like seminal vesicles, to the muscular penis. In many species, this basic plan is considerably complicated by the addition of accessory glands or other structures. The penis lies inside a cavity, and can be everted through an opening on the posterior underside of the animal. It often, although not always, possesses a sharp stylet. Unusually among animals, in most species, the sperm cells have two tails, rather than one.

In most platyhelminths, the ovaries are divided into two regions, one producing the ova, and the other producing specialised yolk cells to nourish the developing embryo. While many turbellarians have this arrangement, some are apparently more primitive. In these latter species, the ovaries are undivided, and the egg cells contain yolk within their own cytoplasm, as is the case in most other animals. In either arrangement, the ovaries possess oviducts that run to a bursa for storing sperm. The bursa is in turn connected to the vagina, which opens in front of the penis. In some cases, there also be other structures for sperm storage, in addition to the bursa, or even a uterus for storage of ripe eggs.

In most species "miniature adults" emerge when the eggs hatch, but a few large species produce plankton-like larvae.

2. Trematoda

Trematoda

Botulus microporus, a giant digenean parasite from the intestine of a lancetfish

Scientific classification

Kingdom:	Animalia
Phylum:	Platyhelminthes
Class:	**Trematoda** Rudolphi, 1808

Subclasses

Aspidogastrea
Digenea

Trematoda is a class within the phylum Platyhelminthes that contains two groups of parasitic flatworms, commonly referred to as "flukes".

Taxonomy and biodiversity

The trematodes or flukes are estimated to include 18,000 to 24,000 species, and are divided into two subclasses. Nearly all trematodes are parasites of mollusks and vertebrates. The smaller Aspidogastrea, comprising about 100 species, are obligate parasites of mollusks and may also infect turtles and fish, including cartilaginous fish.

The Digenea, which constitute the majority of trematode diversity, are obligate parasites of both mollusks and vertebrates, but rarely occur in cartilaginous fish.

Formerly the Monogenea were included in Trematoda on the basis that these worms are also vermiform parasites, but modern phylogenetic studies have raised this group to the status of a sister class within the Platyhelminthes, along with the Cestoda.

Anatomy

Trematodes are flattened oval or worm-like animals, usually no more than a few centimetres in length, although species as small as 1 millimetre (0.039 in) and as large as 7 metres (23 ft) are known. Their most distinctive external feature is the presence of two suckers, one close to the mouth, and the other on the underside of the animal.

The body surface of trematodes comprises a tough syncitial tegument, which helps protect against digestive enzymes in those species that inhabit the gut of larger animals. It is also the surface of gas exchange; there are no respiratory organs.

The mouth is located at the forward end of the animal, and opens into a muscular, pumping pharynx. The pharynx connects, via a short oesophagus, to one or two blind-ending caeca, which occupy most of the length of the body. In some species, the caeca are themselves branched. As in other flatworms, there is no anus, and waste material must be egested through the mouth.

Although the excretion of nitrogenous waste occurs mostly through the tegument, trematodes do possess an excretory system, which is instead mainly concerned with osmoregulation. This consists of two or more protonephridia, with those on each side of the body opening into a collecting duct. The two collecting ducts typically meet up at a single bladder, opening to the exterior through one or two pores near the posterior end of the animal.

The brain consists of a pair of ganglia in the head region, from which two or three pairs of nerve cords run down the length of the body. The nerve cords running along the ventral surface are always the largest, while the dorsal cords are present only in the Aspidogastrea. Trematodes generally lack any specialised sense organs, although some ectoparasitic species do possess one or two pairs of simple ocelli.

Reproductive system

Most trematodes are simultaneous hermaphrodites, having both male and female organs. There are usually two testes, with sperm ducts that join together on the underside of the front half of the animal. This final part of the male system varies considerably in structure between species, but may include sperm storage sacs and accessory glands, in addition to the copulatory organ, which is either eversible, and termed a *cirrus*, or non-eversible, and termed a penis.

There is usually only a single ovary, which is connected, via a pair of ducts to a number of *vitelline glands* on either side of the body, that produce yolk cells. Eggs pass from the ovary into a glandular receptacle called the *ootype* or *Mehlis' gland*, where fertilization occurs. This opens into an elongated uterus that opens to the exterior close to the male opening. The ovary is often also associated with a storage sac for sperm, and a copulatory duct termed *Laurer's canal*.

Life cycles

Almost all trematodes infect mollusks as the first host in the life cycle, and most have a complex life cycle involving other hosts. Most trematodes are monoecious and alternately reproduce sexually and asexually. The two main exceptions to this are the Aspidogastrea, which have no asexual reproduction, and the schistosomes, which are dioecious.

In the definitive host, in which sexual reproduction occurs, eggs are commonly shed along with host feces. Eggs shed in water release free-swimming larval forms that are infective to the intermediate host, in which asexual reproduction occurs.

A species that exemplifies the remarkable life history of the trematodes is the bird fluke, *Leucochloridium paradoxum*. The definitive hosts, in which the parasite multiplies, are various woodland birds, while the hosts in which the parasite grows (intermediate host) are various species of snail. The adult parasite in the bird's gut produces eggs and these eventually end up on the ground in the bird's faeces. Some very fortunate eggs get swallowed by a snail and here they hatch into tiny, transparent larva (miracidium). These larvae grow and take on a sac-like appearance. This stage is known as the sporocyst and it forms a central body in the snail's digestive gland that extends into a brood sac in the snail's head, muscular foot and eye-stalks. It is in the central body of the sporocyst where the parasite replicates itself, producing lots of tiny embryos (redia). These embryos move to the brood sac and mature into cercaria.

Infections

Human infections are most common in Asia, Africa, South America, or the Middle East. However, trematodes can be found anywhere that human waste is used as fertilizer.

Etymology

Trematodes are commonly referred to as *flukes*. This term can be traced back to the Old English name for flounder, and refers to the flattened, rhomboidal shape of the worms.

The flukes can be classified into two groups, on the basis of the system which they infect in the vertebrate host.

- **Tissue flukes** infect the bile ducts, lungs, or other biological tissues. This group includes the lung fluke, *Paragonimus westermani*, and the liver flukes, *Clonorchis sinensis* and *Fasciola hepatica*.

- **Blood flukes** inhabit the blood in some stages of their life cycle. *Blood flukes include species of the genus* Schistosoma*.*

They may also be classified according to the environment in which they are found. For instance, **pond flukes** infect fish in ponds.

3. Digenea

Digenea

Helicometra sp. (Plagiorchiida: Opecoelidae) from the intestine of a Flame Cardinal fish

Scientific classification

Kingdom:	Animalia
Phylum:	Platyhelminthes
Class:	Trematoda
Subclass:	**Digenea** Carus, 1863

Orders

Azygiida
Echinostomida
Opisthorchiida
Plagiorchiida
Strigeidida

Digenea (Gr. *Dis* - double, *Genos* - race) is a subclass within the Platyhelminthes consisting of parasitic flatworms with a syncytial tegument and, usually, two suckers, one ventral and one oral. Adults are particularly common in the digestive tract, but occur throughout the organ systems of all classes of vertebrates. Once thought to be related to the Monogenea, it is now recognised that they are closest to the Aspidogastrea and that the Monogenea are more closely allied with the Cestoda. Around 6,000 species have been described to date.

Morphology

Key features

Characteristic features of the digenea include a syncitial tegument; that is, a tegument where the junctions between cells are broken down and a single continuous cytoplasm surrounds the entire animal. A similar tegument is found in other members of the Neodermata; a group of platyhelminths comprising the Digenea, Aspidogastrea, Monogenea and Cestoda. Digeneans possess a vermiform, unsegmented body-plan and have a solid parenchyma with no body cavity, as in all platyhelminths.

There are typically two suckers, an anterior oral sucker surrounding the mouth, and a ventral sucker sometimes termed the *acetabulum*, on the ventral surface. The oral sucker surrounds the mouth, while the ventral sucker is a blind muscular organ with no connection to any internal structure.

Monostome is a term used to describe worms with one sucker (oral). Flukes with an oral sucker and an acetabulum at the posterior end of the body are called *Amphistomes*. *Distomes* are flukes with an oral sucker and a ventral sucker, but the ventral sucker if somewhere other than posterior. These terms are common in older literature, when they were thought to reflect systematic relationships within the groups. They have fallen out of use in modern digenean taxonomy.

Reproductive system

The vast majority of digeneans is hermaphroditic. This is likely to be an adaptation to low abundance within hosts, allowing the life cycle to continue when only one individual successfully infects the final host. Fertilisation is internal, with sperm being transferred via the cirrus to the Laurer's Canal or genital aperture. A key group of digeneans which are dioecious are the schistosomes. Asexual reproduction in the first larval stage is ubiquitous.

While the sexual formation of the digenean eggs and asexual reproduction in the first larval stage (miracidium) is widely reported, the developmental biology of the asexual stages remains a problem. Electron microscopic studies have shown that the light microscopically visible germ balls consist of mitotically dividing cells which give rise to embryos and to a line of new germ cells that become included in these embryonic stages. Since the absence of meiotic processes is not proven, the exact definition remains doubtful.

Male organs

Protandry is the general rule among the Digenea. Usually two testes are present, but some flukes can have more than 100. Also present are vasa efferentia, a vas deferens, seminal vesicle, ejaculatory duct and a cirrus (analogous to a penis) usually (but not always) enclosed in a cirrus sac. The cirrus may or may not be covered in proteinaceous spines. The exact conformation of these organs within the male terminal genitalia is taxonomically important at the familial and generic levels.

Female organs

Usually there is a single ovary with an oviduct, a seminal receptacle, a pair of vitelline glands (involved in yolk and egg-shell production) with ducts, the ootype (a chamber where eggs are formed), a complex collection of glands cells called *Mehlis' gland*, which is believed to lubricate the uterus for egg passage.

In addition, some digeneans possess a canal called Laurer's Canal, which leads from the oviduct to the dorsal surface of the body. The function of this canal is debated, but it may be used for insemination in some species or for disposal of waste products from reproduction in other species. Most trematodes possess an ovicapt, an enlarged portion of the oviduct where it joins the ovary. It probably controls the release of ova and spaces out their descent down the uterus.

The uterus typically opens into a common genital atrium that also received the distal male copulatory organ (cirrus) before immediately opening onto the outer surface of the worm. The distal part of the uterus may be expanded into a metraterm, set off from the proximal uterus by a muscular sphincter, or it may be lined with spines, as in the Monorchiidae and some other families.

Digestive system

As adults, most digeneans possess a terminal or subterminal mouth, a muscular pharynx that provides the force for ingesting food, and a forked, blind digestive system consisting of two tubular sacs called caeca (sing. caecum). In some species the two gut caeca join posteriorly to make a ring-shaped gut or cyclocoel. In others the caeca may fuse with the body wall posteriorly to make one or more anuses, or with the excretory vesicle to form a uroproct. Digeneans are also capable of direct nutrient uptake through the tegument by pinocytosis and phagocytosis by the syncitium. Most adult digeneans occur in the vertebrate alimentary canal or its associated organs, where they most often graze on contents of the lumen (e.g., food ingested by the host, bile, mucus), but they may also feed across the mucosal wall (e.g., submucosa, host blood). The blood flukes, such as schistosomes, spirorchiids and sanguinicolids, feed exclusively on blood. Asexual stages in mollusc intermediate hosts feed mostly by direct absorption, although the redia stage found in some groups does have a mouth, pharynx and simple gut and may actively consume host tissue or even other parasites. Encysted metacercarial stages and free-living cercarial stages do not feed.

Nervous system

Paired ganglia at the anterior end of the body serve as the brain. From this nerves extend anteriorly and posteriorly. Sensory receptors are, for the most part, lacking among the adults, although they do have tangoreceptor cells. Larval stages have many kinds of sensory receptors, including light receptors and chemoreceptors. Chemoreception plays an important role in the free-living miracidial larva recognising and locating its host.

Life cycles

There is a bewildering array of variation on the complex digenean life cycle, and plasticity in this trait is probably a key to the group's success. In general, the life cycles may have two, three, or four obligate (necessary) hosts, sometimes with transport or paratenic hosts in between. The three-host life cycle is probably the most common. In almost all species, the first host in the life cycle is a mollusc. This has led to the inference that the ancestral digenean was a mollusc parasite and that vertebrate hosts were added subsequently.

The alternation of sexual and asexual generations is an important feature of digeneans. This phenomenon involves the presence of several discrete generations in one life-cycle.

A typical digenean trematode life cycle is as follows. Eggs leave the vertebrate host in faeces and use various strategies to infect the first intermediate host, in which sexual reproduction does not occur. Digeneans may infect the first intermediate host (usually a snail) by either passive or active means. The eggs of some digeneans, for example, are (passively) eaten by snails (or, rarely, by an annelid worm), in which they proceed to hatch. Alternatively, eggs may hatch in water to release an actively swimming, ciliated larva, the miracidium, which must locate and penetrate the body wall of the snail host.

After post-ingestion hatching or penetration of the snail, the miracidium metamorphoses into a simple, sac-like *mother sporocyst*. The mother sporocyst undergoes a round of internal asexual reproduction, giving rise to either *rediae* (sing. redia) or *daughter sporocysts*. The second generation is thus the daughter parthenita sequence. These in turn undergo further asexual reproduction, ultimately yielding large numbers of the second free-living stage, the *cercaria* (pl. cercariae).

Free-swimming cercariae leave the snail host and move through the aquatic or marine environment, often using a whip-like tail, though a tremendous diversity of tail morphology is seen. Cercariae are infective to the second host in the life cycle, and infection may occur passively (e.g., a fish consumes a cercaria) or actively (the cercaria penetrates the fish).

The life cycles of some digeneans include only two hosts, the second being a vertebrate. In these groups, sexual maturity occurs after the cercaria penetrates the second host, which is in this case also the definitive host. Two host life-cycles can be primary (there never was a third host) as in the Bivesiculidae, or secondary (there was at one time in evolutionary history a third host but it has been lost).

In three-host life cycles, cercariae develop in the second intermediate host into a resting stage, the *metacercaria*, which is usually encysted in a cyst of host and parasite origin, or encapsulated in a layer of tissue derived from the host only. This stage is infective to the definitive host. Transmission occurs when the definitive host preys upon an infected second intermediate host. Metacercariae excyst in the definitive host's gut in response to a variety of physical and chemical signals, such as gut pH levels, digestive enzymes, temperature, etc. Once excysted, adult digeneans migrate to more or less specific sites in the definitive host and the life cycle repeats.

Evolution

The evolutionary origins of the Digenea have been debated for some time, but there appears general agreement that the proto-digenean was a parasite of a mollusc, possibly of the mantle cavity. Evidence for this comes from the ubiquity of molluscs as first intermediate hosts for digeneans, and the fact that most aspidogastreans (the sister group to the Digenea) also have mollusc associations. It is thought that the early trematodes (the collective name for digeneans and aspidogastreans) likely evolved from rhabdocoel turbellarians that colonised the open mantle cavity of early molluscs.

It is likely that more complex life cycles evolved through a process of terminal addition, whereby digeneans survived predation of their mollusc host, probably by a fish. Other hosts were added by until the modern bewildering diversity of life cycle patterns developed.

Important families

The Digenea includes at least 50 families. Below is a list of the more commonly encountered ones.

Acanthocolpidae	Derogenidae	Haplosplanchnidae	Paramphistomidae
Accacoeliidae	Dicrocoeliidae	Hemiuridae	Paragonimidae
Allocreadiidae	Didymozoidae	Heronomidae	Philophthalmidae
Angiodictyidae	Diplostomidae	Heterophyidae	Plagiorchiidae
Apocreadiidae	Echinostomatidae	Lecithasteridae	Sanguinicolidae
Atractotrematidae	Enenteridae	Lepocreadiidae	Schistosomatidae
Azygiidae	Fasciolidae	Microphallidae	Sclerodistomidae
Bivesiculidae	Faustulidae	Monorchiidae	Strigeidae

Bucephalidae	Fellodstomidae	Nasitrematidae	Syncoeliidae
Campulidae	Gorgoderidae	Notocotylidae	Tandanicolidae
Cryptogonimidae	Gyliauchenidae	Opecoelidae	Transversotrematidae
Cyclocoelidae	Haploporidae	Opisthorchiidae	Zoogonidae

There are some digenean families that are either basal to or *incertae sedis* among the orders listed above:

- Acanthocollaritrematidae
- Echinoporidae
- Gekkonotrematidae
- Gyliauchenidae
- Jubilariidae
- Meristocotylidae
- Mesotretidae

Human digenean infections

Only about 12 of the 6,000 known species are infectious to humans, but some of these species are important diseases afflicting over 200 million people. The species that infect humans can be divided into groups, the schistosomes and the non-schistosomes.

Schistosomes

The Schistosomes occur in the circulatory system of the definitive host. Humans become infected after free-swimming cercaria liberated from infected snails penetrate the skin. These dioecious worms are long and thin, ranging in size from 10 to 30 mm in length to 0.2 to 1.0 mm in diameter. Adult males are shorter and thicker than females, and have a long groove along one side of the body in which the female is clasped. Females reach sexual maturity after they have been united with a male. After mating the two remain locked together for the rest of their lives. They can live for several years and produce many thousands of eggs.

The four species of schistosomes that infect humans are members of the genus *Schistosoma*.

Human Schistosomes		
Scientific Name	**First Intermediate Host**	**Endemic Area**
Schistosoma mansoni	*Biomphalaria* spp.	Africa, South America, Caribbean, Middle East

Schistosoma haematobium	*Bulinus* spp.	Africa, Middle East
Schistosoma japonicum	*Oncomelania* spp.	China, East Asia, Philippines
Schistosoma intercalatum	*Bulinus* spp.	Africa

Non-schistosomes

There seven major species of non-schistosomes that infect humans are listed below. People become infected after ingesting metacercarial cysts on plants or in undercooked animal flesh. Most species inhabit the human gastrontestinal tract, where they shed eggs along with host feces. *Paragonimus westermani*, which colonizes the lungs, can also pass its eggs in saliva. These flukes generally cause mild pathology in humans, but more serious effects may also occur.

Human non-Schistosomes			
Scientific Name	**First Intermediate Host**	**Mode of Human Infection**	**Endemic Area**
Fasciolopsis buski	*Segmentina* sp.	Plants	Asia, India
Heterophyes heterophyes	*Pirinella*	Mullet, Tilapia	Asia, Eastern Europe, Egypt, Middle East
Metagonimus yokogawaii	*Semisulcospira* sp.	Carp, Trout	Siberia
Gastrodiscoides hominis	*Helicorbis* sp.	Plants	India, Vietnam, Philippines
Clonorchis sinensis	*Bulinus* sp.	Fish	East Asia, North America
Fasciola hepatica	*Galba truncatula*	Plants	Central America, North America, South America
Paragonimus westermani	*Oncomelania* sp.	Crabs, crayfish	Asia

4. Aspidogastrea

Aspidogastrea

Lobatostoma manteri, an Aspidogastrean parasite of Australian fishes.

Scientific classification

Kingdom:	Animalia
Phylum:	Platyhelminthes
Class:	Trematoda
Subclass:	**Aspidogastrea**

Families

Aspidogastridae
Multicalycidae
Rugogastridae
Stichocotylidae

The **Aspidogastrea** (Ancient Greek: ἀσπίς *aspis* “shield”, γαστήρ *gaster* “stomach/pouch”) is a small group of flukes comprising about 80 species. It is a subclass of the trematoda, and sister group to the Digenea. Species range in length from approximately one millimeter to several centimeters. They are parasites of freshwater and marine molluscs and vertebrates (cartilaginous and bony fishes and turtles). Maturation may occur in the mollusc or vertebrate host. None of the species has any economic importance, but the group is of very great interest to biologists because it has several characters which appear to be archaic.

Morphology

Shared characteristics

Shared characteristics of the group are a large ventral disc with a large number of small alveoli ("suckerlets") or a row of suckers and a tegument with short protrusions, so-called "microtubercles".

Larval physiology

Larvae of some species have ciliated patches. Those of *Multicotyle purvisi* have four patches on the anterior side of the posterior sucker and six at the posterior side, those of *Cotylogaster occidentalis* have an anterior ring of eight and a posterior ring of six, while larvae of *Aspidogaster conchicola*, *Lobatostoma manteri*, *Rugogaster hydrolagi* lack cilia altogether. Larvae of some species hatch from eggs, others do not.

Excretory system

Like most platyhelminthes, aspidogastreans use flame cells as an excretory mechanism. The two excretory bladders are located dorsally, on the anterior side of the posterior sucker, connected to ducts, and three flame cell "bulbs" on each side of the body; the ducts contain cilia to aid the flow of excreta.

Nervous system

Aspidogastreans have a nervous system of extraordinary complexity, greater than that of related free-living forms, and a great number of sensory receptors of many different types. The nervous system is of great complexity, consisting of a great number of longitudinal nerves (connectives) connected by circular commissures. The brain (cerebral commissure) is located dorsally, in the anterior part of the body, the eyes dorsally attached to it. A nerve from the main connective enters the pharynx and also supplies the intestine. Posteriorly, the main connective enters the sucker.

Sensory receptors are scattered over the ventral and dorsal surface, the largest numbers occurring on the ventral surface, at the anterior end and on the posterior sucker. Electron-microscopic studies revealed 13 types of receptors.

Life cycles

Their life cycle is much simpler than that of digenean trematodes, including a mollusc and a facultative or compulsory vertebrate host. There are no multiplicative larval stages in the mollusc host, as known from all digeneans.

Host specificity of most aspidogastreans is very low, i.e., a single species of aspidogastrean can infect a wide range of host species, whereas a typical digenean trematode is restricted to few species (at least of molluscs). For example, *Aspidogaster* *conchicola* infects many species of freshwater bivalves belonging to several families, as well as snails, many species of freshwater fishes of several families, and freshwater tortoises.

Life cycles have been elucidated for a number of species. *Lobatostoma manteri* is an example of a species which has obligate vertebrate hosts. Adult worms live in the small intestine of the snubnosed dart, *Trachinotus blochi* (Teleostei, Carangidae), on the Great Barrier Reef. They produce large numbers of eggs which are shed in the faeces. If eaten by various prosobranch snails, larvae hatch in the stomach, and—depending on the species of snail—stay there or migrate to the digestive gland where they grow up to the preadult stage which has all the characteristics of the adult including a testis and ovary.

Evolutionary relationships

Digenean trematodes have been cultured in various, complex, media. However, their parasitic stages die soon in water. Aspidogastreans may survive for many days or even weeks outside a host in simple physiological saline solution). For example, adult *A. conchicola* survived in water for a fortnight, and in a mixture of water and saline solution for up to five weeks. *L. manteri* extracted from fish could be kept alive for up to 13 days in dilute sea water in which they laid eggs containing larvae infective to snails. This has led to the suggestions that aspidogastreans are archaic trematodes, not yet well adapted to specific hosts, which have given rise to the more "advanced" digenean trematodes, and that the complex life cycles of digenean trematodes have evolved from the simple ones of aspidogastreans.

Synapomorphies of the trematodes are presence of a *Laurer's Canal*, a posterior sucker (transformed to an adhesive disc in the Aspidogastrea), and life cycles involving molluscs and vertebrates. DNA studies have consistently supported this sister group relationship. The question of whether vertebrates or molluscs are the original hosts of the trematodes, has not been resolved.

This view is supported by the evolutionary relationships of the hosts which these two subclasses utilise. The hosts of aspidogastreans include chondrichthyan fishes (sharks, rays and chimaeras), a group that is 450 million years old, whereas the digeneans, are known from teleost fishes (210 million years old) as well as from various "higher" vertebrates; very few species have invaded chondrichthyans secondarily.

Families within the Aspidogastrea

Rohde (2001) distinguish four families of Aspidogastrea:

- The **Rugogastridae** include a single genus, *Rugogaster*, with two species from the rectal glands of holocephalan fishes. It is characterised by a single row of rugae (transverse thickenings of the body surface), numerous testes, and two caeca. Species of all other families have a single caecum and either one or two testes.

- The **Stichocotylidae** include the single species *Stichocotyle nephropis* from the intestine of elasmobranchs. It has a single ventral row of well separated suckers.
- The **Multicalycidae** include the single genus *Multicalyx* from the intestine of holocephalans and elasmobranchs. It is characterised by a single ventral row of alveoli.
- The **Aspidogastridae** includes species infecting molluscs, teleosts and turtles. The ventral adhesive disc bears either three or four rows of alveoli. Rohde distinguishes three subfamilies of Aspidogastridae, the *Rohdellinae*, *Cotylaspidinae* and *Aspidogastrinae*.

Gibson further recognized two orders, the **Aspidogastrida** with the single family Aspidogastridae, and the **Stichocotylida** including the Stichocotylidae, Multicalycidae and Rugogastridae. However, similarities between species of these two orders are so great that distinction at the level of orders does not seem justified.

5. Monogenea

Monogenea

Dermophthirius, a microbothriidmonogenean parasitic on elasmobranchs

Scientific classification

Kingdom:	Animalia
Phylum:	Platyhelminthes
Class:	**Monogenea** Carus, 1863

Subclasses

Monopisthocotylea
Polyopisthocotylea

Monogenea (adj. monogenean) are a group of largely ectoparasitic members of the flatworm phylum Platyhelminthes, class **Monogenea**.

Characteristics

Monogenea are small parasitic flatworms mainly found on skin or gills of fish. They are rarely longer than about 2 cm. A few species infecting certain marine fish are larger and marine forms are generally larger than those found on fresh water hosts. Monogeneans lack respiratory, skeletal and circulatory systems and have no or weakly-developed oral suckers.. Monogenea attach to hosts using hooks, clamps and a variety of other specialized structures. They are often capable of dramatically elongating and shortening as they move. Biologists need to ensure that specimens are completely relaxed before measurements are taken.

Like all ectoparasites monogeneans have well developed attachment structures. The anterior structures are collectively termed the **prohaptor**, while the posterior ones are collectively termed the **opisthaptor**. The posterior opishaptor with its hooks, anchors, clamps etc. is typically the major attachment organ.

Like other flatworms, Monogenea have no true body cavity (coelom). They have a simple digestive system consisting of a mouth opening with a muscular pharynx and an intestine with no terminal opening (anus). Generally, they also are hermaphroditic with functional reproductive organs of both sexes occurring in one individual. Most species are oviparous but a few are vivarous. Monogenea are Platyhelminthes and therefore are among the lowest invertebrates to possess three embryonic germ layers—endoderm, mesoderm, and ectoderm. In addition, they have a head region that contains concentrated sense organs and nervous tissue (brain).

Systematics and Evolution

The ancestors of Monogenea were probably free-living flatworms similar to modern Turbellaria. According to the more widely accepted view, "rhabdocoel turbellarians gave rise to monogeneans; these, in turn, gave rise to digeneans, from which the cestodes were derived. Another view is that the rhabdocoel ancestor gave rise to two lines; one gave rise to monogeneans, who gave rise to digeneans, and the other line gave rise to cestodes" .

There are about 50 families and thousands of described species.

Some parasitologists divide Monogenea into two (or three) subclasses based on the complexity of their haptor: Monopisthocotylea have one main part to the haptor, often with hooks or a large attachment disc, whereas Polyopisthocotylea have multiple parts to the haptor, typically clamps. These groups are also known as Polyonchoinea and Heteronchoinea, respectively. Polyopisthocotyleans are almost exclusively gill-dwelling blood feeders, whereas Monopisthocotyleans may live on the gills, skin and fins.

Monopistocotylea include:

- Genus *Gyrodactylus,* which has no eyespots and is viviparous.
- Genus *Dactylogyrus,* which has four eyespots and is oviparous. This is one of the largest metazoan genera, with at least 970 species.
- Genus *Neobenedenia,* which is much larger and lives on the skin of many tropical marine species, causing problematic infections in marine aquaria.

All of which can cause epizootics in freshwater fish when raised in aquaculture.

Polyopisthocotylea include:

- Genus *Diclidophora,* which is primarily found in marine fish and primitive freshwater fish like sturgeons and paddlefish.

- Genus *Protopolystoma,* found in aquatic clawed toads (*Xenopus* species).

Ecology and life cycle

Monogeneans possess the simplest life cycle among the parasitic platyhelminths. They have no intermediate hosts and are ectoparasitic on fish (seldom in the urinary bladder and rectum of cold-blooded vertebrates). Although they are hermaphrodites, the male reproductive system becomes functional before the female part. The eggs hatch releasing a heavily ciliated larval stage known as an *oncomiracidium*. The *oncomiracidium* has numerous posterior hooks and is generally the life stage responsible for transmission from host to host.

No known monogeneans infect birds, but one (*Oculotrema hippopotami*) infects mammals, parasitizing the eye of the hippopotamus.

6. Cestoda

Cestoda

Scolex of *Taenia solium*

Scientific classification

Kingdom:	Animalia
Phylum:	Platyhelminthes
Class:	**Cestoda**

Subclasses and orders

Cestodaria
Amphilinidea
Gyrocotylidea
Eucestoda

Aporidea
Caryophyllidea
Cyclophyllidea
Diphyllidea
Lecanicephalidea
Litobothridea
Nippotaeniidea
Proteocephalidea
Pseudophyllidea
Spathebothriidea
Tetraphyllidea
Trypanorhyncha

Cestoda (**Cestoidea**) is the name given to a class of parasitic flatworms, commonly called **tapeworms**, of the phylum Platyhelminthes. Its members live in the digestive tract of vertebrates as adults, and often in the bodies of various animals as juveniles. Over a thousand species have been described, and all vertebrate species can be parasitised by at least one species of tapeworm. Several species parasitise humans after being consumed in underprepared meat such as pork (*T. solium*), beef (*T. saginata*), fish (*Diphyllobothrium* spp.), or in food prepared in conditions of poor hygiene (*Hymenolepis* spp. or *Echinococcus* spp.).

T. saginata, the beef tapeworm, can grow up to 12 m (40 ft); other species may grow to over 30 m (100 ft).

Anatomy

Scolex

The worm's *scolex* ("head") attaches to the intestine of the definitive host. In some species, the scolex is dominated by bothria (tentacles), which are sometimes called "sucking grooves", and function like suction cups. Other species have hooks and suckers that aid in attachment. Cyclophyllid cestodes can be identified by the presence of four suckers on their scolex.

While the scolex is often the most distinctive part of an adult tapeworm, it is often unnoticed in a clinical setting as it is inside the patient. Thus, identifying eggs and proglottids in feces is important.

Body systems

The main nerve centre of a cestode is a cerebral ganglion in its scolex. Motor and sensory innervation depends on the number and complexity of the scolex. Smaller nerves emanate from the commissures to supply the general body muscular and sensory ending. The cirrus and vagina are innervated, and sensory endings around the genital pore are more plentiful than other areas. Sensory function includes both tactoreception and chemoreception. Some nerves are only temporary. These are in the proglottids, and stop working with a detach.

Proglottids

The body is composed of successive segments (*proglottids*). The sum of the proglottids is called a strobila, which is thin, and resembles a strip of tape. From this is derived the common name "tapeworm". Like some other flatworms, cestodes use flame cells (protonephridia), located in the proglottids, for excretion. Mature proglottids are released from the tapeworm's posterior end and leave the host in feces.

Because each proglottid contains the male and female reproductive structures, they can reproduce independently. Some biologists have suggested that each should be considered a single organism, and that the tapeworm is actually a colony of proglottids.

The layout of proglottids comes in two forms, craspedote, meaning proglottids are overlapped by the previous proglottid, and acraspedote which indicates a non-overlapping conjoined proglottid.

Once anchored to the host's intestinal wall, the tapeworm absorbs nutrients through its skin as the food being digested by the host flows past it and it begins to grow a long tail, with each segment containing an independent digestive system and reproductive tract. Older segments are pushed toward the tip of the tail as new segments are produced by the neckpiece. By the time a segment has reached the end of the tail, only the reproductive tract is left. It then drops off, carrying the tapeworm eggs to the next host.

Reproduction and life cycle

True tapeworms are exclusively hermaphrodites; they have both male and female reproductive systems in their bodies. The reproductive system includes one or many testes, cirrus, vas deferens and seminal vesicle as male organs, and a single lobed or unlobed ovary with the connecting oviduct and uterus as female organs. There is a common external opening for both male and female reproductive systems, known as genital pore, which is situated at the surface opening of the cup-shaped atrium. Even though they are sexually hermaphroditic, self-fertilization is a rare phenomenon. In order to permit hybridization, cross-fertilization between two individuals is often practiced for reproduction. During copulation, the cirrus one individual connects with that of the other through the genital pore, and then exchange their spermatozoa.

The life cycle of tapeworms is simple in the sense that there are no asexual phases as in other flatworms, but complicated in that at least one intermediate host is required as well as the definitive host. This life cycle pattern has been a crucial criterion for assessing evolution among Platyhelminthes. Many tapeworms have a two-phase life cycle with two types of host. The adult *Taenia saginata* lives in the gut of a primate such as a human. Proglottids leave the body through the anus and fall onto the ground, where they may be eaten with grass by animals such as cows. In the cow's body, the juvenile form migrates and establishes as a cyst in body tissues such as muscles, rather than the gut; they cause more damage to this host than the intestinal form to its host. The parasite completes its life cycle when the grass-eater is eaten by a compatible carnivore—possibly a human with a preference for raw meat—in whose gut the adult *Taenia* establishes itself.